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OF THE
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OF
NEW SOUTH WALES

FOR THE YEAR

1948

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* Actual date of issue, 26th October, 1948.

ANNUAL GENERAL MEETING.

WEDNESDAY, 31st MARCH, 1948.

The Seventy-third Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 31st March, 1948.

Dr. G. D. Osborne, President, occupied the Chair.

The minutes of the preceding Annual General Meeting (26th March, 1947) were read and confirmed.

PRESIDENTIAL ADDRESS.

The past year has been a rather remarkable one in the Society's history, for the following reasons: there has been a change in the Secretaryship; Dr. Jensen, the Macleay Bacteriologist, has resigned from his post; and while during the first part of the year only one Macleay Fellowship was being held, in the latter part of the year even this position was vacated by the resignation of Miss Lascelles, and thus for a period of four months the Society possessed no research staff. Its 1947 research programme therefore was on a very reduced scale.

The general meetings have proved quite successful with rather small but consistent attendances. In order to make the meetings more attractive, several lecturettes were arranged, these being given by Dr. Walkom, Dr. Ida Brown and Mr. F. D. McCarthy, and a symposium on "Physiology of Plant Disease" was held, the chief speakers being Professor N. A. Burges, Dr. N. H. White and Dr. R. N. Robertson.

The printing of the PROCEEDINGS is now practically up to date, Parts 5 and 6 of Volume 72 having been issued on 15th January, 1948. Volume 72 consists of 386 + xxx pages, 23 plates and 218 text-figures and maps. It is somewhat larger than Volume 71. Printing costs have unfortunately now risen approximately 40 per cent., Parts 5 and 6 being at the increased rate. Your Council has been exploring sources for monetary assistance in printing papers, especially with regard to communicated papers. There are sufficient manuscripts in hand for Parts 1 to 4 of Volume 73.

Exchanges received from scientific societies and institutions totalled 1,349 for the year, an increase of 120 over the previous year, but rather less than in the pre-war years.

The Library has been cleaned and the Society is proceeding with the rationalization scheme jointly arranged with the Royal Society of New South Wales. It has not been possible to get any books bound, although enquiries have been made, lack of skilled bookbinders being one of the difficulties. The store-room has been cleaned and a new set of shelving erected. The Society's stock of PROCEEDINGS has been rearranged in an orderly manner.

The nett return from Science House exceeded that received in any previous year. No final decision has been made regarding a combined Reading Room and Library in the proposed extension of Science House, nor has the matter of this extension advanced any further.

The numerical strength of the Society at 28th February, 1948, was: Ordinary Members, 184; Honorary Member, 1; Life Members, 14; Corresponding Members, 3; total, 202. During the year 23 new members were elected, and the Society lost four members through resignation and arrears in subscription, and two by death.

Torrington Hawke Pincombe, B.A., who had been a member since 1920, died on 18th July, 1947. Mr. Pincombe was born at Braidwood in 1867 and engaged in the teaching profession. He taught at many places, but chiefly at Broken Hill and in the Newcastle District. He always had a great interest in natural history, being an amateur geologist, chiefly interested in fossil insects and plants. He collected much material for

the late John Mitchell and was always ready to help younger men in a practical way, especially in their field work.

Alfred Jefferis Turner, who died in Brisbane on 29th December, 1947, was born in Canton, China, on 3rd October, 1871. He graduated at the University of London, taking his M.B. in 1884 and M.D. in 1886. Arriving in Australia in 1888, he settled in Brisbane in the following year, where he practised his profession until a few years prior to his death. He was the Australian authority on the *Lepidoptera* and specialized in the moths of that Order. His first paper, which dealt with *Micro-Lepidoptera* from Moreton Bay, appeared in 1894, while his first paper in the PROCEEDINGS of our Society was published in 1902. His last paper to the Society, dealing with the *Oecophoridae*, No. XIV, appeared in the PROCEEDINGS, Parts 3 and 4, 1947. Another large paper on the *Boarmiadae* was published last year in the *Proceedings of the Royal Society of Queensland*. In all he had published 116 papers and articles, of which 43 appeared in our PROCEEDINGS. Dr. Turner had collected extensively in all Australian States, including Tasmania.

It was with very great regret that your Council accepted the resignation of Dr. N. S. Noble from the position of Secretary to the Society. Dr. Noble resigned on 31st July, 1947, in order to take up the position of Editor of the new *Australian Journal of Scientific Research*, which has been established by the Council for Scientific and Industrial Research and the Australian National Research Council.

As Secretary, Dr. Noble served this Society, of which he is a Life Member, with efficiency and distinction since 1941, when he succeeded Dr. Walkom. His discretion, friendliness and capacity in scientific affairs won him the warm regard of every councillor of the Society, as well as of many others. He was particularly interested and energetic concerning the management of Science House, of which he was the Honorary Secretary-Treasurer, and our present augmented income from this source has reached its high figure largely due to his efforts. We thank Dr. Noble for his whole-hearted interest in the affairs of the Society during the difficult war years, and wish him every success in his new position.

After widely advertising the position of Secretary the Council appointed Dr. Dorothy Carroll as successor to Dr. Noble. Dr. Carroll was formerly mineralogist and soil mineralogist at the Government Chemical Laboratories, Perth. She graduated in Arts and Science at the University of Western Australia with First Class Honours in Geology in 1932, and later proceeded to the Imperial College, London, where she specialized in sedimentary petrography, working under Professors Boswell and Brammall, and received the Ph.D. degree and D.I.C. for research on soils from the Western Australian goldfields. Returning to Australia in 1936, Dr. Carroll became a Commonwealth Research Fellow in Geology, transferring in 1941 to the Chemical Laboratories in order to undertake the completion of the late Dr. E. S. Simpson's "Minerals of Western Australia", which is now in the press. From 1942 to 1945 she was in charge of the mineral information section in connection with the prosecution of the war. Dr. Carroll has published a considerable number of papers on soils and sedimentary rocks in local and overseas journals. We look forward to her having a successful occupancy of the Secretaryship and offer her our best wishes.

We are grateful as a Society to the Hon. Treasurer, Dr. Walkom, for his oversight of the Society's financial affairs throughout the year. We congratulate him on the award of the Clarke Memorial Medal for 1948.

The Society's Research Staff:

The Society has been unfortunate in losing its Macleay Bacteriologist, Dr. H. L. Jensen, who resigned in order to return to Denmark as Director of Plant Culture (Department of Bacteriology) at Lyngby. H. L. Jensen was appointed Bacteriologist to the Society in 1929. He graduated in Agriculture at the Royal Agricultural and Veterinary College in Copenhagen in 1920, and later was appointed Assistant in Research at the State Laboratory of Plant Culture, Lyngby. In 1927 he received a Rockefeller Foundation Fellowship and proceeded to Rothamsted, where he undertook research in the Department of Soil Bacteriology, and it was from there that he applied for the

position of Macleay Bacteriologist, for which he was strongly recommended by Sir John Russell, a recommendation seen to be amply justified in the quality of the research he carried out for the Society, and in the thirty odd papers he published in the PROCEEDINGS. The first research that Jensen did as Macleay Bacteriologist was an investigation of the microbiology of arid and irrigated soils, and this led to work on many associated problems in connection with the decomposition of organic matter by soil organisms. This period of his work culminated in 1939 when his paper on "Nitrogen Economy of Australian Wheat Soils, with particular reference to New South Wales", was approved for the degree of Doctor Agronomiae by the Royal Agricultural and Veterinary College, Copenhagen. From then on he was actively engaged on various aspects of nitrogen fixation by clovers and medics, more especially with regard to the effect of minor elements such as molybdenum and vanadium on the nitrogen-fixing power of nodule organisms. During the war, at the request of the Council for Scientific and Industrial Research, Dr. Jensen carried out investigations on the micro-organisms responsible for the dew-retting of flax under Australian conditions; also on antiseptics for prevention of contamination of blood sera; rot-proofing of tent canvas; prevention of bacterial spoilage of canned foods; deterioration and preservation of military equipment in the tropics; and many other fields.

This Society has lost a tireless and enthusiastic research officer who as Macleay Bacteriologist gained a world-wide reputation for original work of a very high standard, and thus brought great prestige to our Society.

The Society re-appointed Miss June Lascelles to a Linnean Macleay Fellowship in Biochemistry, from which she resigned in August, 1947, in order to proceed to Oxford as an 1851 Exhibitioner. During the tenure of her Fellowship in 1946 and 1947 Miss Lascelles continued investigations on the oxidation of molecular hydrogen by bacteria. She obtained an M.Sc. in 1946, and has published a number of joint papers on her investigations.

I have pleasure in reminding you that the Council appointed Miss Muriel Morris, B.Sc., and Miss Mary Tindale, M.Sc., to Macleay Fellowships in Zoology and Botany respectively, tenable from the 1st January, 1948.

Miss Morris will study seasonal changes in the plankton of the Hawkesbury Estuary and the biology of the oyster beds. Miss Tindale will undertake a revision of Australian Pteridophyta with special reference to New South Wales genera.

On account of the difficulty of attracting applicants for Macleay Fellowships, chiefly due to the depressed economic value of the Fellowship stipends, the Council has made special enquiry from its solicitors as to the best method of securing a variation of the Macleay Will, in order to make possible the payment of higher stipends to Macleay Fellows, and also to enlarge the field of eligibility on the part of applicants. The enquiries in connection with the matter are not yet completed.

During the year we received 25 bound copies of the text of the report upon the Natural History Survey of Kosciusko State Park carried out in 1946. Also one copy complete with two maps and 44 photographs was made available for a period by the Park Trust. Eventually several illustrated copies will be available for distribution to the institutions specially concerned.

Throughout the year Dr. W. R. Browne, Vice-President, has been on leave of absence from the Council on account of his being in England for the purpose of seeing the David Book on the Geology of the Commonwealth of Australia through the press. You will be glad to know that this work is moving on rapidly and the greater part of the book is now in proof form.

We offer congratulations to Mr. W. H. Maze, formerly member of Council, on his appointment as Deputy Registrar in the University of Sydney.

In August last a very successful meeting of the Australian and New Zealand Association for the Advancement of Science was held in Perth, when a record number of members attended. This congress was notable in several ways, and it is of special interest to this Society to note that the meeting marked the retirement of Dr. Walkom from the position of Honorary General Secretary, which he had held for 21 years. It

would be difficult adequately to assess the great contribution Dr. Walkom has made to Science during his long service to the Association. This outstanding work was signally recognized by his election as President of the Association for the Hobart meeting to be held in January, 1949, and we offer him hearty congratulations.

It is of further interest to the Society that in selecting a successor to Dr. Walkom the Council of the Association chose Professor N. A. Burges, a member of our Council. We offer Professor Burges our best wishes for a happy and successful tenure of this important position.

A REVIEW OF SOME ASPECTS OF THE STRATIGRAPHY, STRUCTURE AND PHYSIOGRAPHY
OF THE SYDNEY BASIN.*

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INTRODUCTION.

For the second part of my address I have chosen a local field with fairly wide scope for geological meditation. My decision to deal with the natural history of terrains surrounding the Sydney area is based mainly on the fact that except for palaeontological researches the Triassic rocks, during the first third of this century, were largely neglected; and since that time, few noteworthy pieces of work have been done upon them. In this latter category are particularly to be mentioned two investigations upon the Stratigraphy and Structure of the Hawkesbury and Narrabeen Series. These were conducted for purposes of applied geology, but have yielded a great deal of geological data from which, when made available to the general reader, many trends of geological research can develop. I refer to work carried out upon—

- (a) oil and gas possibilities in the Hawkesbury-Hunter sector,
- (b) the geology of a site for the Warragamba Dam in connection with the Sydney Water Supply.

The results of these researches have thrown into relief our inadequate knowledge of much of the geology of the Sydney Basin.

The main purposes of this address may be stated to be as follows:

- (a) To discuss several aspects of Triassic geology (somewhat arbitrarily selected), stressing the Hawkesbury Sandstone.
- (b) To record the writer's personal observations and views.
- (c) In particular, to lay emphasis upon the environmental conditions attending sedimentation during Narrabeen and Hawkesbury times.
- (d) To review some of the later tectonic and physiographic history of the Sydney Basin.
- (e) To indicate some of the many problems awaiting solution.
- (f) Above all, to endeavour to awaken a greater local interest in the study of Sediments than now exists.

It is hoped that this paper may assist geologists, professional and amateur, including those who teach in colleges and schools, who may require some kind of conspectus of Triassic problems. Much of the information in this address has been culled from

* The author gratefully acknowledges financial help from the Commonwealth Research Grant in connection with this work.

sources not readily accessible to many who have an interest in the geology of the Sydney Basin. Many observations recorded have been made by the author in recent months and partly all through his geological career, as Sydney District geology has been a continuing interest since his student days, when many items were studied in a somewhat immature way.

In connection with the two investigations mentioned above I am particularly indebted to—

- (a) an unpublished D.Sc. Thesis by Dr. H. G. Raggatt, and
- (b) to Mr. L. L. Waterhouse, Dr. W. R. Browne and Mr. D. G. Moye for discussing some aspects of the geology of the Warragamba district (with kind approval of the Metropolitan Water, Sewerage and Drainage Board).

Mr. Moye has kindly conducted me over some of this area.

Two Science graduands of the University, Messrs. B. P. Webb and P. B. Andrews, have assisted me considerably in field work, and the results of some work carried out by them under my supervision have been freely drawn upon for this address.

It is earnestly hoped that workers of the future, especially younger people, will devote attention to some of the many geological secrets bound up with the Triassic System of Central Eastern New South Wales.

THE NARRABEEN SERIES.

STRATIGRAPHY.

H. G. Raggatt (1938) has traced the geological investigation of the Narrabeen Series, referring to the work and writings of Clarke, Wilkinson, David, Carne, Harper, Dun, Walton and Bonney, Etheridge, Walkom, Willan, Culey and Garretty. His own important contribution (based upon superior field work) embodies the establishment of a detailed stratigraphy for the Narrabeen Series in the Gosford–Wyong region, a correlation of this standard section with other districts in the Sydney Basin, and (in addition to other matters) a discussion of the evolution of the region in Narrabeen time.

Summarized, the stratigraphy of the Narrabeen Series in the Wyong–Gosford region, as established by Raggatt, is as follows:

Upper Narrabeen	560 feet	maximum thickness
Middle Narrabeen	850 feet	„ „
Lower Narrabeen	880 feet	„ „

Total 2,290 feet

One important criterion used in the subdivision has been the occurrence of two well-defined group-horizons of red, purple or chocolate coloured sediments, known (in previous decades) as the Chocolate Shales (upper horizon) and the Cupriferous Tuffs (lower unit). Raggatt puts the top of the Middle Narrabeen at the top of the Upper Red Beds, and the top of the Lower Narrabeen at the top of the Lower Red Beds.

Observations by the Author.

In order to examine and compare the sedimentational environment of the Narrabeen rocks on either side of the central portion of the coastal outcrop of the Cumberland Basin, I have measured very detailed sections in the Avalon–Bilgola, and the Bulgo–Stanwell Park–Coalcliff districts. Excellent, practically unweathered, sections can be obtained in these localities although the southern cliff sections are almost inaccessible in places and require a considerable amount of precarious climbing. Nevertheless magnificent exposures are to be seen, giving the whole of the Narrabeen at Coal Cliff, and the greater portion of it at Bulgo and Undola.

The Avalon–Newport sections were partly measured in the company of Professor Leo A. Cotton, while assisting him in directing field studies of the Geology III students of 1944. The southern sections were partly determined by Messrs. Webb and Andrews.

The Upper Narrabeen in the Collaroy–Avalon District.

Several geologists have at various times made stratigraphical and mineralogical observations upon the Narrabeen strata of this area, but apart from Miss Culey's work

(1932 and 1938) and certain palaeontological papers, little has been published. H. G. Raggatt states (in his thesis) that Mr. A. W. Atkinson carried out mapping in the region and was able to recognize the Mangrove Sandstone in the Pittwater area. (The Mangrove Sandstone is a prominent marker-bed in the Wyong region.)

Sections at Careel Head and Bilgola Head.—In the cliff faces to the north of Avalon the Upper Narrabeen is well exposed, and its relations to the Hawkesbury Series satisfactorily displayed. A very careful instrumental survey of the cliff section north of St. Michael's Cave revealed the following general stratigraphy of the Upper Narrabeen, beginning at the base of the Hawkesbury Sandstone.

	Thickness in feet.
Group A. Sandy shales and flaggy sandstone	90
Group B. Massive sandstone	46
Group C. Rhythmically banded shales and sandstones ..	35
Group D. Second massive sandstone band	42
Group E. Rhythmic sandy shales and shales	33

These groups of rocks were seen to be characteristic of a good deal of the region. It was noted, however, that as one traced the series southward the group-horizons marked C and D united to form a fairly uniform section, chiefly medium-grained and arenaceous. This unit could be traced easily through much of the country between Careel Head and Newport. The higher sandstone band, horizon B, could also be traced, and indeed was carefully mapped at Newport. This sandstone is evenly bedded, finely laminated, and occasionally cross-bedded. It often outcrops in large freestone beds and has been largely quarried. The sandstone possesses a few thin bands of shale and a little shale-breccia, and some peculiar ironstone nodules. It is immediately overlain by soft shaly sandstones with notable slabs of fine sandstone about two feet thick. The main sandstone is exposed in the roadside quarry just above, and to the south of Bilgola Beach. From here it swings around through North Newport Head and is seen in a quarry above and north of Hillside Road. Farther south it has been mapped to the hill behind the Workers' Educational Association property. It can be seen at intervals in the rounded hills near Warriewood, and thus is a useful datum. It will probably be found equivalent to the Mangrove Sandstone.

At the track to St. Michael's Cave horizon D gives the following detailed section:

Brown sandstone, with little current bedding and honeycomb weathering	15 feet
Lenses of conglomerate with pebbles up to 5 inches, but averaging 2 inches; lenses mostly 2 chains long and 2 feet thick	12 feet
Rhythmically bedded sediment:	
Shale	3 feet
Sandstone	1 foot
Shale	3 feet
Sandstone	2 feet
Shale	1 foot
Sandstone	1½ feet
Shale	1 foot
Pebbly ironstone	2½ feet
	15 feet

Horizon E gave the following details:

Fine laminated sandstone, with sweeping current-bedding, "slump" and "rill" structure, honeycomb weathering	9 feet
Rhythmic alternating sandy shale and sandstone:	
Shale	2 feet
Sandstone	2 feet
Shale	3 feet
Sandstone	1 foot
Shale	2 feet
Sandstone	4 feet
Shale	3 feet
Sandstone	2 feet
Shale	1 foot
Sandstone	4 feet
	24 feet

} Climatically zoned.

(Some graded bedding present.)

Below Horizon E, the following are the details:

Fine laminated sandy shale with plant remains	5 feet
Purplish sandstone with odd shale fragments and swirl-marks	1 foot
Alternation of purplish sandstone and shale	4 feet
Coarse sandstone with washouts and pockets of carbonaceous shale	3 feet
Fine sandstone with a little purplish shale-breccia. Ripple-mark well developed	6 feet
Clay shale	1 foot
Fine black shales with good ripple-mark and plant remains	20 feet
Fine shaly sandstone with ripple-mark	6 feet
Red climatically banded sandstone	2 feet
Flaky sandy shale	10 feet
Swirl-marked shale	2 feet
Fine current bedded shaly sandstone	3 feet
Black shale	1 foot
Ripple marked laminated sandstone	2 feet
Fine sandy shale with plant remains	3 feet
Black sandstone and ironstone nodules	2 feet
Worm-tracks in quartzitic sandstone	3 feet
Rhythmic sandy shale	4 feet
Ironstone shales	1 foot
Sandstones and shales	2 feet
Fine laminated sandstone	4 feet
Shaly sandstone with cylindrical sandcasts	3 feet

The section is completed by measuring the rhythmic sandstone-shale group at Bilgola which underlie the "sandcast structures", thus:

Ironstone	8 inches
Sandstone	10 inches
Shale	2 inches
Sandstone	12 inches
Shale with carbonate of Fe	3 inches
Current-bedded sandy shale	9 inches
Sandstone	4 inches
Shale	4 inches
Sandstone	2 inches
Shale	8 inches
Sandstone	10 inches
Fine ripple-marked purplish sandstone	10 feet
Total Upper Narrabeen	350 feet

Chocolate shales (Middle Narrabeen).

Three horizons need further amplification:

(a) The massive sandstone, Horizon D, is beautifully current-bedded and in a specimen to be seen near St. Michael's track the most delicately developed current-bedding may be studied. The specimen is 12 feet long by 4 feet, by about 2 feet thick.

Four separate layers of current-bedded character bespeak the capricious acts of vigorous but spasmodic currents. Some of the cross-bedding is of the type due to contemporaneous erosion of topset beds. One wedge-section, however, shows what is rare in the Sydney District, viz., a complete double-curved series of laminae in the sandstone.

(b) The massive sandstones often have their continuity broken by conglomerates which possess variable grainsize up to five inches. Many pebbles, about 2 inches in diameter, are of red jasper, green jasperoid rock, volcanic rocks, quartz and black chert. The matrix is gritty.

Associated with the pebbles are irregular fragments of ferruginous shale which have been carried along with the pebbles, deposited in current-bedded layers and gradually diminished by swirl action.

(c) The abundance of vertical cylindrical and almost cylindrical sand-casts up to five inches in length in a fine quartzitic carbonaceous sandstone below St. Michael's Cave (see stratigraphical table) is a notable occurrence. These intriguing structures are due to the preservation of casts in sand of the numerous reed-roots which grew in a swamp. Further south isolated larger reed-casts of ironstone are found. This horizon is traceable for a fair distance along the Careel Head sector, and is to be distinguished from the worm-track horizon, which is stratigraphically above it. The latter

is traceable southward right to Long Reef, and has proved a useful indicator in the Pittwater-Collaroy region.

Problems of the Sedimentary Environment.—In seeking to interpret the sections along the Avalon-Newport coast and thus arrive at some idea of the evolving Narrabeen Basin, one finds the following types of environment are required:

First, there were mostly copious supplies of slightly ferruginous fine-grained sand which was deposited at shallow depths, and extensively ripple-marked. Some of the ripple-structures were exposed to the air, then overwhelmed by mud, which in turn was cracked by drying-out and filled in with sand again.

Secondly, at frequent intervals, coarse shingle of jasper, etc., was supplied, and with this material came red-ironstone and shaly iron-oxide which had been developed in a quiet basin, because of the fine texture exhibited.

Thirdly, current-bedding was developed in non-ripple-marked sandstone where lack of strength of current and capricious direction-changing were the order of the day.

Fourthly, a frequent rhythmic control of climate and partly of lithology must have operated from the many rhythmic sediments which are more sandy than shaly.

Fifthly, a delicate control in the production of the rhythmic fine clay-shale and fine sandstone is called for at Bilgola South.

All these demands during Upper Narrabeen sedimentation immediately give us a measure of the partial problem of explaining the changing environment in a depositional area which was some distance from any shore. Further considerations about these matters will be given below.

The Sections at Coal Cliff and Undola.—A general section was measured by John Mackenzie (1897) at Coal Cliff, which gives a thickness of 939 feet for the Narrabeen Series. The cliffs above the classic place of discovery of coal by Bass and Flinders give a splendid section. The whole of the cliff face is unstable, however, and is much cut by joints and faults. Due to alternations of shales and heavy sandstones, the region is dangerous, and the roadway (Prince's Highway) below is in constant danger of subsidence. Already several major slips have occurred and occasional serious rock-falls have taken place. The weaker shales overlain by great vertical sections of heavy sandstone have been undercut by erosion, necessitating strengthening by the erection of brick and stone retaining walls.

The following is the detailed section determined by Messrs. Webb and Andrews and the writer:

Lower Narrabeen.

Lower Chocolate Shales.

Chemically rhythmic greenish and purple shales with about 20 lenses of calcareous tuff (see detailed description)	70 feet
Typical finely-bedded, mostly chocolate-coloured, shales with greenish tuff, and slightly sandy phases	40 feet
Lower chemically rhythmic horizon	30 feet
Chocolate shales, greenish tuffs, and fine brownish sandstone	30 feet
	170 feet

These rocks form a sloping section between more or less vertical cliff sections of Lower Narrabeen and overlying Middle Narrabeen. Away from the cliffs these Lower Chocolate Shales and associated rocks form a marked step in the topography due to easy weathering. They are also responsible for the great amphitheatre in the topography of Stanwell Park. Particularly due to their faulted and jointed condition have they been easily eroded. They are fairly constant in total thickness, and actually thicker than in the Heathcote Bore farther north and close to the areas of thickening Narrabeen Series.

The nature of rhythmic banding in the Chocolate Shales and Tuffs should be investigated. This feature is found on the all but inaccessible cliffs above Bulgo shore. Here there are seventeen lenses of bluish rock, which under the microscope is seen to be calcareous tuff. The lenses are about 3 to 6 feet long with general thickness of 5 inches, but up to a maximum of 10 inches. These lenses alternate with and are

embedded in chocolate shale and greenish fine tuff. They indicate a nicely balanced repetition of supply of materials and chemical control in an undisturbed zone of sedimentation.

Lower Narrabeen (continued).

Massive yellow sandstone with conglomerate in coarse lenses. Some current-bedding present	120 feet
Bluish shale and lenses of tuff	25 feet
Conglomerate with current-bedding, passing into sandstone. Hard ironstone lenses and wash-outs present	20 feet
Weak shale zone	10 feet
Shale with ironstone	25 feet
Shale with plant remains	8 feet
Sandstone with current-bedding	10 feet
Shale (bluish)	6 feet
Massive sandstone with some current-bedding	45 feet

Total for Lower Narrabeen 439 feet

It is easy to correlate and compare certain horizons between Undola and Coal Cliff. Thus the lower conglomerates at Bulgo and Undola are coarser than at Coal Cliff. They have pebbles up to 9 inches in diameter, and there is a greater amount of strong current structure. Coarse graded bedding amongst the pebbles is seen, and there is a marked band of intraformational breccia a little less than halfway down from the top of the main conglomerate horizon.

Middle Narrabeen (at Undola).

Upper Chocolate Shales with a little blue shale	45 feet
Purplish grits	10 feet
Fine laminated sandstone and tuff	20 feet
Shales	45 feet
Rhythmic alternations of strong sandstone and shale	300 feet
Massive sandstone	12 feet
Sandstone with current-bedding and shaly layers	25 feet

Total 457 feet

In this series the most notable feature is the rugged outcrop of the 300 feet of sandstone and associated shaly layers. Sometimes heavy conglomerate lenses occur, and also large fragments of shale are associated with the conglomerates at their base.

The Upper Chocolate Shales, so well exposed on the hilltops near the summit of Bald Hill, show several white bands of clay-shale, and some narrow breccias.

The 20-foot laminated sandstone weathers spheroidally and is strongly developed in the southern part of National Park. In the sandstone at the base of the Middle Narrabeen above Undola Head a beautiful section of textural interest was noted. This showed no less than sixteen units of current-bedded phases overlying one another in sequence. The false bedding had very fine texture and the average thickness of the inclined units was eight inches.

Upper Narrabeen.—These rocks are best studied on the summit of the hills above Undola Head, and also at Garie and Burning Palms Beach areas. They can be seen also in the National Park. They vary greatly in thickness and it is suggested that some extensive washouts have diminished their thickness considerably.

The succession below the Hawkesbury Sandstone is as follows:

Transitional but fairly massive sandstone (yellowish)	9 feet
Shaly sandstones with current-bedding and lenses of conglomerate	20 feet
Massive sandstone	6 feet
Shale layers in sandstone	10 feet
Reddish yellow sandstone with much iron-oxide and lenses of tuff	30 feet

Total 75 feet

It will be seen that the Upper Narrabeen has thinned greatly as compared with the north side of the eastern Cumberland Basin. However, one notes a resemblance between the Bilgola sandstone and one of the sandstones at Stanwell Park.

The Sedimentary Environment.

Full details of measured sections have been given above in order that some discussion may be made of environmental factors during the accumulation of various phases of the series.

It is clear that one of the most significant sedimentary attributes of the present central coastal strip of the Narrabeen Series is the rhythmic character of the sequence.

A major rhythm is indicated in the succession of—

- (1) Sandstone, shales with subordinate conglomerates and tuffs.
- (2) Lower Red Beds.
- (3) Sandstones, shales and conglomerates.
- (4) Upper Red Beds.
- (5) Sandstones, sandy shales, conglomerates and tuffs.

Pronounced rhythms of the second order are commonly developed in many levels of the sequence, while what may be termed rhythms of the third order are seen where fine lithological and textural features are repeated over and over again in an otherwise broadly uniform horizon. This indicates the transporting agencies and the controls in the sedimentary area have fluctuated rather regularly.

The whole question of the changing physical environment through the Narrabeen Basin is not being discussed here. Such a grand theme has been ably presented by Raggatt although an extension of his observations and his discussion would be greatly welcomed by students interested in the evolution of the Triassic Period in New South Wales.

For the purpose of this address (which stresses the local field, to some extent) the following cyclic controls may be envisaged:

- (a) Tectonic movements in both the areas of supply and of accumulation.
- (b) Stream behaviour in the supply of sediment to lacustrine areas.
- (c) Chemical changes and cycles in the waters of deposition, particularly with regard to zones with calcareous development.
- (d) Climatic cycles—particularly in relation to (a) colour of sediments, (b) manner of transport (aeolian or aqueous), and (c) volume of river waters.

That each of these controls has fluctuated in its incidence and intensity is clear.

Apart from the rhythmic character so persistent in the series, a fairly marked variety of environments is also indicated. Conglomeratic deposits with coarse current-bedding and irregular shale breccias point to a swift-flowing medium in deltaic areas. Thus fluvial action is strongly represented.

The content of true tuff and of partly redistributed tuff, seen in the Upper and Lower Narrabeen, indicates a volcanic environment from time to time. But in the absence of massive volcanic rocks or of any disturbance in the tuffs, it is clear that we have to visualize freely falling material derived from places distant from the scene of sedimentation.

Transitional environments are indicated in many places, e.g., where coarse conglomerates up to 4 feet thick gradually merge into fine laminated sandstones with discordant current-bedded relationships.

Then again, some of the fine ashen-coloured clays in amongst the sandstone may be due to accumulation of fine material blown by wind on to shallow delta zones.

In the areas under review, the *vertical* variation is quite remarkable when one considers the significance of changing textural and lithological types. The *lateral* variation is also noteworthy, but careful mechanical analyses would probably show that the variation of significant minerals was fairly systematic and not statistically random (cf. Allen, 1945).

In the rocks under discussion the cross- or current-bedding is often beautifully and finely drawn, but discontinuous. At other times it is of rather coarse texture and continuous. These two types indicate, respectively, the operation of—

- (a) active, but not voluminous, currents that have oscillated in their positions in the delta area;

- (b) strong currents of fairly constant volume and direction which have built up the uniform-slope type of foreset lamination.

On the whole the current-bedding in the Narrabeen Series does not show a noticeable preferred orientation for the direction of dip of the layers, but the greatest frequency of dip was towards the interval south to south-east.

The local impersistence of many lithologic types and the relatively common occurrence of scour-and-fill relationships, especially near Bulgo, indicate conditions of varying current strength and fluctuation in the water-body controlling precipitation of sediment.

Since a considerable portion of the shaly layers of the Narrabeen, especially the Lower and Middle Stages, shows complete leaching (even in core samples that have not been exposed to weathering), it is suspected that derivation has been from pre-existing sedimentary material.

The Heavy or Resistant Mineral Suites.—The only analytical work done upon the mineralogical content of the Narrabeen Series is that by Alma G. Culey (1932). This work was of a pioneering kind, and worthy of much commendation, because of the comprehensiveness of the investigation, and the sound sedimentary principles evinced in the account given. From this study Miss Culey has been able to determine a numerous mineralogical content, and to make certain deductions which are summarized below.

The minerals determined in the Narrabeen-Pittwater and Garie-Coal Cliff districts were as follows: Chalcopyrite, magnetite, pyrite, picotite, anatase, rutile, zircon, apatite, rhombohedral carbonate, ilmenite, tourmaline, barytes, biotite, muscovite, quartz, felspar.

The later work by Culey (1938) upon the mineralogy of the Upper Permian sediments led her to observe the possibility of some of the Narrabeen Series having been produced by the re-distribution of Permian sediment. This conception is in agreement with the evidence of complete leaching already mentioned.

An interesting feature of Narrabeen mineralogy is the presence of several minerals in the authigenic condition. The three forms of titanium oxide, rutile, brookite and anatase all occur in this way.

The development of a wide variety of minerals in sediments, allegedly by authigenic growth, raises a rather knotty problem. It throws into relief the complicated nature of the chemical and physical reactions that go on in ground waters at fairly low temperatures. Many minerals recorded as authigenic are of complex composition, with many atoms present. The marshalling of these at various times in sedimentary environments presents a problem that has hardly been treated in anything like a full and satisfactory manner by petrographers. The possible effect of hydrothermal waters in helping the genesis of resistant minerals in sediments has been discussed fairly fully, but it is clear from the wealth of data that a great variety of minerals can be authigenically produced by groundwater action after deposition. It should be the aim of those investigating any terrain to look for any possible correlations between nature of authigenic minerals, nature of probable provenance of the sediments, and the hydrological history of the sediment, as far as it is possible to determine.

In discussing this analytical mineralogical work (while in no way under-estimating the great value of the investigation) it must be pointed out, in respect of any analyses of our sedimentary rocks, that conclusions about provenance and sedimentational environment cannot be rigidly based on the examination of individual specimens from many areas. A large number of specimens of the *same* horizon in a fairly restricted lateral interval should be analysed before frequency-values can be used for correlative purposes in a great basin of deposition. The full statistical analysis is really essential if a complete picture is to be obtained of the changing environment of deposition, and the variation of supply of certain assemblages of minerals. The very important implication of the post-depositional instability of some minerals hitherto regarded as infallible indices also gives a warning about the subtleties bound up with correlation and interpretation of heavy mineral data (this last matter has recently been stressed in another place, Osborne, 1944, 24).

THE PROBLEM OF THE RED BEDS OF THE NARRABEEN SERIES.

No feature of the Narrabeen Series, taken as a whole, is so vividly remembered by geologists and others who have observed this terrain, than the occurrence of the red, purple or chocolate-coloured horizons, generally of shaly character. These rocks impart a special scenic quality to landscapes where vegetation has not been strongly established, as for example on actively-eroded slopes and cliffs. Quarries in the Red Beds also are of distinctive appearance.

The occurrence of a red or purplish colouration in sediments has always intrigued geologists and the traditional view for a considerable period was to regard such coloured sediments as indicators of arid or semi-arid climates (desert conditions in extreme cases) in the distributive provinces whence the sediments were derived.

It was considered that the conditions existing in warm, arid regions would allow the development of abundant haematite rather than the persistence of pale-coloured carbonate of iron and other ferrous compounds. Reducing agents in a well vegetated environment would maintain reduction and preclude red colouration.

In later years more careful study of the problem, coupled with observations on colours in modern soils and sediments, has led to recognition of the fact that red colouration may be developed in several ways, thus representing varied environments in regions both of erosion and of accumulation.

The question of the red condition being absent at time of deposition and subsequently produced by oxidation, has received attention from several workers. Quite a number of cases are known where greyish and greenish shales (in bore cores, for example) have turned red on exposure.

The stratigraphy of the Narrabeen Series proclaims a frequently recurring control that produced red or chocolate-coloured sediment. While many minor layers occur, two main horizons outweigh all others in importance, and their stratigraphical positions have been broadly known for a long time. Actually, although the Lower have been called the Cupriferous Tuffs, the presence of copper compounds has been responsible for either bright blue or green tints in patchy development, or a dull brownish colour in the case of metallic material. It seems quite unnecessary to link the purplish colouration causally with the presence of copper compounds in these beds. Perhaps underlying the assembling of copper in the sediments were some processes that helped to stamp the red character on much of the so-called cupriferous shale.

Narrabeen rocks with ferrous compounds have green and greyish colours and alternate with the red beds. It is not always a case of the red beds containing more iron than the paler strata, but that the proportion of Fe_2O_3 to FeO is greater in the former.

A review of some papers on Red Beds is pertinent here, in order to give a setting to the Narrabeen problem. Although some of these writings date back a considerable way, many valid and significant statements are to be found in them.

Tomlinson (1916) in one of the earliest theoretical and exhaustive contributions, was of the opinion that the bulk of the red colouration came from ferruginous residual soils. He visualised mechanical sediments of fine residual material, and also red-coated sand grains, being swept down as stream deposits into basins of accumulation. This was the picture for the red beds of western U.S.A. He suggested the periodic development of red beds was related to climatic and topographic changes dependent on orogenic episodes. He stressed the possibility of the retention of the red colour in sediments deposited in, but not derived from, an arid or semi-arid region.

G. E. Dorsey (1926), in dealing with the Triassic of eastern U.S.A., emphasized the contrast between the presence of ferric oxide (with associated water-content) as an ingredient of a sediment, and the actual occurrence of hydrated ferric oxide (turgite) and anhydrous ferric oxide (haematite) both of which are red and impart colouration to formations. Dorsey thought that the essential controls operating in the accumulation of red beds (of primary pigmentation) were—

- (1) The development of ferric oxide by rock decomposition and disintegration.

- (2) The production of red soil and dust in a well-drained environment that is generally humid and warm (tropical to sub-tropical) by dehydration of ferric compounds.
- (3) The deposition of reddish sediment in an environment devoid of abundant reducing agencies, particularly the absence of organic material expected in marine territory.

He thus concluded that red beds are mostly continental in origin. He opposed an origin for red beds that assumed complete marine location, because of the attendant reduction performed by decayed organic material.

Twenhofel (1939) in his survey of the problem says:

"the weight of opinion at the present time refers them (i.e., Red Beds) to deposition in either a continental environment or an environment bearing some close relation to the sea.

". . . red residual soils are considered the provenance of most of the Red Beds of which the sediments were red at the time of deposition. . . .

". . . The most favourable condition for deposition and preservation of colour of red sediments on land areas lies between the extremes of some degree of moderate rainfall and semi-aridity under relatively high temperature conditions."

In dealing with the red beds of the Trias-Jura of the Rocky Mountain area, Branson (1927) postulated a marine origin for the greater part of the terrain, basing his decision upon the associated sedimentary features which were persistent and characteristic of marine deposition.

Some non-marine red beds were the result of continental conditions, these having much less regularity in their associated sedimentary attributes.

Reeside (1929), in discussing the work of Branson, concludes that a sub-aeolian origin is to be attributed to a large part of the terrain.

P. E. Raymond (1927) also dealt with the red beds of the Eastern States. Bringing to bear a critical approach, including the consideration of the life of various periods concerned, he concluded that humid, rather than arid, conditions were requisite for red beds, which should accumulate rapidly. Like others at the time of his writing (about 20 years ago), he drew attention to the limited knowledge of the origins and functions of the main iron compounds in sediments. The last two decades have not provided much new information about the iron compounds that will solve the red bed problems. R. D. Reed (1929), in his comprehensive account of the Sespe Formation, in California, traversed the question of red colouration, and inclined to the view of primary red colour and development in a subsiding basin, not continually under the water, but fed by large streams. He was opposed to a "desert" or "aridity" criterion of formation.

Coming now to the problem of the Narrabeen Beds, we derive help from the literature, but the significant features which give some individuality to these red beds:

- (1) The colour is frequently deep purplish. This is not quite the normal colouration in other sediments.
- (2) The great area of development; these red beds are present from the Lower Illawarra in the south-west along the western and northern margins of the Basin, and (on the evidence of bores) through all the central part of the Basin:

Red beds similar to the paler varieties of the Sydney Basin occur in the Lorne Basin, north of Taree, and even further extended areas of development are known.

- (3) The shales are very evenly textured, having a fairly uniform set of characters, such as Sp. Gr., fracture, plasticity, etc. Further, through the whole of the areas of outcrop, the shales show, in the partially weathered condition, a uniform patchy partial reduction of the iron, in the intensely oxidized (or dehydrated) mass. This property indicates uniformity of reaction to katamorphic action over a great area.

- (4) The rhythmic or recurrent mode of development is characteristic of large areas.
- (5) The associated Narrabeen sediments often are in contrast with the shales, and with one another, texturally and lithologically.
- (6) As recorded above, the Lower Chocolate Shales are marked by a beautiful cyclic deposition of lenses of calcareous rock alternating with the fine shale. Microscopic examination of this rock shows that it is a very fine re-distributed tuff with much basic content, the cementing-medium being calcite and/or siderite.

At this stage the writer wishes to stress his belief that the red colour was original in the whole of the horizons he has studied. This was borne in on me after examining the cores of the Narrabeen Series at Warragamba. A certain amount of deepening of the purple or chocolate colour no doubt has followed exposure, but the pigmentation was effected before the accumulation of the Hawkesbury sandstone. To postulate wholesale exposure of the Narrabeen series by uplift of the Basin would lead to tectonic difficulties. The Narrabeen Lake was a very extensive structure which underwent subsidence probably at a very steady rate, as indicated by the resistant mineral suites in several regions. To produce red colour in pale sediments by exposure of the sediment would involve several oscillations of the whole basin, with much the same amplitude of movement. For this to be conducted synchronously so as to control sedimentation in various sectors of the Basin, raises great difficulty.

Chemical Composition.—Three analyses of typical shale are given below:

TABLE 1.

	A.	B.	C.
SiO ₂	36.42	38.98	49.48
Al ₂ O ₃	31.48	28.00	33.92
Fe ₂ O ₃	15.50	14.39	} 0.11
FeO	0.45	0.98	
MgO	0.36	0.36	abs.
CaO	0.60	0.15	0.12
Na ₂ O	0.24	0.08	0.10
K ₂ O	0.09	0.18	0.44
H ₂ O+	10.19	10.38	12.33
H ₂ O-	1.77	3.60	1.49
CO ₂	—	0.22	—
TiO ₂	2.24	2.05	2.20
P ₂ O ₅	0.12	0.06	0.07
MnO	0.02	0.04	tr.
SO ₃	0.18	0.01	abs.
Cl	0.12	0.15	tr.
Cr ₂ O ₃	—	0.06	—
NiO	—	0.01	—
CuO	—	0.11	—
BaO	—	tr.	—
ZrO ₂	—	0.01	—
0.058 = FeS ₂	—	0.09	—
CoO, PbO, ZnO, F, SrO, LiO ₂ ..	—	abs.	—
	99.78	99.91	—
Less O for Cl	0.02	0.04	—
	99.76	99.87	100.26

A. Chocolate Shale, Helensburgh, N.S.W. *Ann. Rept. Dept. Mines, N.S.W.*, 1917, p. 182.

B. Chocolate Shale, Long Reef, near Sydney, N.S.W. *J. Roy. Soc. N.S.W.*, XL, 1906, p. 155.

C. Shale, Careel Bay, Pittwater. *Ann. Rept. Dept. Mines, N.S.W.*, 1916, p. 223.

It will be noted that the analyses are not those of igneous rocks, and therefore the rather traditional view held for so long by Sydney geologists that the red beds were essentially tuffs must be discarded. Certainly *some* volcanic material is present.

In concluding this section, the writer would point out an acute difficulty about these enigmatical beds. This is the necessity for postulating geological conditions that could provide transport and the spreading-out of fine material over thousands of square miles, with the retention of a uniformity of texture and colour, and a fairly even base and upper surface in most areas.

The problem of supply alone is formidable, for it seems to lead one to assume that climatic cycles produced red regolith in the whole of the environs of the Narrabeen Basin, so that a constancy of lithological type and an equivalence of climatic variation was maintained at several stages in the evolution of the Narrabeen sub-system.

We realize, therefore, that a first-line problem awaits solution. It will need to be tackled by the employment of modern methods of sedimentology and geochemistry. Comparative studies upon modern red residual deposits will help, but a great deal of field work is still needed to detect the possible occurrence of significant chemical and climatic rhythms in the thicker units of the chocolate-coloured types.

THE HAWKESBURY SANDSTONE. (Hawkesbury Series.)

INTRODUCTION.

From the earliest days of the colony of New South Wales the Hawkesbury Sandstone has figured more or less conspicuously in the everyday life of many inhabitants of Sydney and surrounding country. This has been on account of its dominant place in the scenery, and of its great importance, in earlier days, as a building stone and general engineering material. Even in spite of the coming of modern methods of building and road construction, the Hawkesbury Sandstone still enjoys a considerable measure of usefulness in various minor ways, such as for foundations, garden ornamentation, and the building of balustrades and abutments.

The ubiquitous outcropping of the sandstone in the Sydney Basin, producing sterile, rugged country, the relative simplicity of its mineral constitution, and for the most part, its monotonous lithological character and texture have, in the last few decades, produced an indifference toward, and almost a contempt for this rock series on the part of local geologists, except for one or two notable researches dealing with fauna and flora, and a vital geologico-engineering investigation already referred to above.

One can understand the development of this kind of apathy since any extended researches into the origin of the Hawkesbury Sandstone would involve long and patient work by the methods of sedimentary petrography. Little work of this character has been done here and there are very limited opportunities to obtain training in Australia in such fields of research.

Further, with the limited number of geologists working in New South Wales, there has been little chance in past years, and especially in the early portion of the century, to devote much time to Triassic problems since pressing investigations upon the Coal Measures and other resources of the State have occupied the attention of governmental and to some extent of academic geologists for a long time. Then it is hardly necessary to say that igneous and metamorphic rocks attract the young researcher more readily than do sediments and in general provide better research-dividends.

A BRIEF CHRONOLOGICAL ACCOUNT OF GEOLOGICAL INVESTIGATION OF THE HAWKESBURY SANDSTONE (MAINLY SINCE 1860).

To assist any workers of the future who may wish to carry out research upon some aspects of the Hawkesbury Sandstone, this brief account may be of use, as no connected summary of progress of work upon the Hawkesbury Series is available. (Forty years ago R. S. Bonney (now Mr. Justice Bonney) carried out much work on the Triassic rocks of the Sydney region, but unfortunately his main results were never published. I have had the opportunity of seeing Bonney's microscope slides and a synoptic statement of his Triassic work).

In the present paper it is not proposed to refer to all the early scientific writings in which the Hawkesbury Sandstone is mentioned. In some of these the statements have little value. However, before taking the period about 1860 when the distinguished

W. B. Clarke wrote an account of this formation, it will be advisable to record comments of some early visitors to these shores. (It must not be forgotten that in three important monographs of the Geological Survey of New South Wales, and in a famous Presidential Address by Professor David something of an historical approach to the subject of Triassic geology is provided. Further, Morrison (1903) also gave selected bibliographies on the early Triassic researches; however, nothing comprehensive has been attempted.)

Darwin (1844, 1846), in the account of his visit to New South Wales in 1836, noted the following:

- (a) The glistening of the sandstone. He says: "I was surprised at observing that, in some specimens, nearly all the grains of quartz were so perfectly crystallized with brilliant facets that they evidently had not in their *present* form been segregated in any previously existing rock."
- (b) The current-bedding, which he ascribed to gigantic ripples on the sea floor, later truncated by wave action and covered by horizontal material.
- (c) Shale fragments in the sandstone which he considered had been partly consolidated and broken up by currents.
- (d) A regional dip in the sandstone plateau surface which is approximately parallel to the dip of the sandstone.
- (e) That the sandstones at Lapstone Hill represent the original boundary of the deposit.
- (f) The great gorges of the Blue Mountains are to be attributed partly to original submarine spaces between banks of sediment, later partly excavated.

J. D. Dana (1849) made some references to the sandstone which he examined while visiting Australia in 1840. He called it the "Sydney Rocks".

J. B. Jukes (1847) visited Australia and travelled with Clarke, mainly on horseback, making some observations that impress one nowadays, when one realizes the disadvantages they experienced in the difficulty of travelling and the absence of geological knowledge of the colony. Jukes described the sandstone as 700–800 feet thick, and resembling the Millstone Grit. The occurrence of shale partings and the variable texture were recorded.

Although the descriptions and classification of the Mesozoic Rocks of New South Wales, given by W. B. Clarke in his "Remarks upon the Sedimentary Formations of New South Wales" (3rd Ed., 1870, and 4th Ed., 1878) are generally cited or quoted by workers reviewing Triassic geology, it is important to note the first connected account by Clarke of the Hawkesbury Sandstone is given in his "Southern Goldfields" (1860, p. 248). Here he refers to them as Hawkesbury Rocks and includes a little shale at the top, in spite of his having already described the Wianamatta Beds. His account of the Hawkesbury embodies the following points:

- (a) Series consists of quartzose grits and sandstones 800–1,000 feet thick.
- (b) Presence of pebbles of varied type, and also of mica, graphite and particles of titaniferous iron.
- (c) "Much of the sand consists of crystalline quartz with facets that reflect the sunlight very brilliantly, making the ground full of sparkling points."
- (d) Presence of concretions, of seams of haematite and of much ferruginous content.
- (e) Occurrence of casts of ligneous matter, impressions of ferns and of fishes in brown shaly beds.
- (f) Structural arrangement includes fissured and jointed (particularly with strike N 10° E) horizontal or undulating layers.

Clarke mentions that Sir Thomas Mitchell described the Hawkesbury Sandstone as producing "a world of sterility and stone-quarries".

In the Sedimentary Formations (1878) the earlier information is amplified. He still calls them the Hawkesbury Rocks and refers again to the glistening sand grains and mentions imperfect crystals of quartz. He refers to the cement which may be ferruginous or argillaceous. He regards the muscovite and graphite as allogenic. He also mentions the false bedding.

Clarke thus laid a good stratigraphical and lithological foundation for the Triassic, although this really was the outcome of a long and bitter controversy on the stratigraphical position of our productive coal measures.

Shortly after the appearance of Clarke's fourth edition of the "Sedimentary Formations" several papers came from the pen of C. S. Wilkinson. The more important of these appeared in *Mineral Products of New South Wales* from year to year, but particularly in 1879 and again in 1882.

In the latter year Wilkinson gave an excellent summary of New South Wales geology in the form of a chapter entitled "Notes on the Geology of New South Wales". In this summary the Hawkesbury Series is dealt with comprehensively. It should be noted carefully that these papers of Wilkinson appeared prior to Tenison-Woods' long paper on the Hawkesbury Series.

Wilkinson (in the 1879 and 1882 papers) initiated the view that the angular fragments and ill-assorted boulders sometimes seen in the Hawkesbury Sandstone were due to glacial action. He had to defend this theory, and always emphasized that Professor Julian Van Haast supported him.

A summary of Wilkinson's view on the Hawkesbury Sandstone is as follows:

- (a) Possesses variations in texture.
- (b) The current-bedding is in varying directions with angles up to 22° for the inclined laminae.
- (c) Iron oxide and black oxide of manganese present.
- (d) Patchy development of thin streaks and masses of coal.
- (e) Impersistent shale beds up to 20 feet long and 20 feet thick, often passing into shale-breccia of glacial origin.
- (f) Imbricate structure in the shale fragments indicates water transport operating from the south-west.
- (g) Master joints occurred which affected erosion, the chief direction of strike being north-north-east.
- (h) The surface of the Hawkesbury Sandstone was contemporaneously eroded before the deposition of the Wianamatta.
- (j) The possibility of the sandstone having been derived from a western mountain range.

This last observation was probably the first contribution to the question of provenance of the Hawkesbury Series.

Considerable research was now applied to the local geology and the next step to be noted here was the appearance of a long paper by Rev. J. E. Tenison-Woods (1882). The dominant theme in this monograph was the aeolian origin of the Hawkesbury Sandstone. Although Tenison-Woods eventually abandoned this theory, from an historical point of view it is important to summarize the results of his work at this stage. In this way the antecedents of later work are appreciated. It should be remembered also that his colleagues regarded him highly as a man and a geologist.

The paper was certainly one of the most extended treatises that had yet been presented on any sedimentary formation in New South Wales. The author traversed many aspects of the subject, stressing wind-agency wherever he could connect it with the particular attribute of the Hawkesbury Sandstone under discussion. He was the first to refer to "herring bone" structure, due to the association of opposed current-bedded layers. He showed extremely careful observation, but apparently gradually receded from employing a balanced deductive treatment of his data.

I propose to quote extensively regarding Tenison-Woods' conclusions. He listed fourteen decisions which he had reached. They were as follows:

1. That the Hawkesbury sandstone is a wind-blown formation, interspersed with lagoons and morasses, with impure peat.
2. That there has been no upheaval, but rather a subsidence, which probably extends from the base of the range to the sea.
3. That the peculiar lamination of the beds is due to the angle at which dry sand slips and rests when blown by the wind.

4. The beds of ironstone represent vegetable matter destroyed in oxidizing the iron, and this is why so few plant remains are found.
5. The irregular layers of the sandstone formation probably represent what was a tranquil portion of the surface for a time, on which there may have been a vegetable growth now represented by ironstone bands.
6. The smaller gravel may be wind-blown; the larger may have been derived from creeks. This is also the origin of the fragments of shale. The creeks have undermined them and broken them up.
7. Conglomerates may have been derived from stony deserts, such as we have in the centre of Australia. They represent all the stones of a sandhill district from which the sand has been blown away.
8. The precipitous cliffs of the Blue Mountains are the hard central cores of sandhills, the loose portions of which have been easily blown or washed away.
9. That in all respects the sandstone is like many desert formations of the interior.
10. That a large arid or desert region has existed in Australia in Mesozoic times, while to the north and north-west there was a Cretaceous sea.
11. That this desert was terminated by the outpouring of vast quantities of volcanic rock, which altered the drainage and probably changed the climate.
12. We have no means of knowing the eastern limits of this ancient desert, as there has been subsidence on that side.
13. This formation differs but slightly from other and more extensive aerial ones in other countries, especially in Mexico, China, Arabia, etc.
14. There is no evidence of ice-action, and all the physical features are against such a supposition.

This monographic contribution to the Royal Society of New South Wales was immediately taken up in reply by leaders in geological and general scientific thought at that time.

C. S. Wilkinson (1882, pp. 91-97) discussed the fourteen points and opposed most of them. He attacked strongly the aeolian theory and gave as his testimony the view that the current-bedding was mostly aqueous, citing angles of rest for sands accumulated in air and in water, and referring to experiments.

He placed his finger on a very weak spot in Tenison-Woods' conclusions regarding the pebbles and gravel in the Hawkesbury Sandstone, and showed the great difficulties of provenance under the author's theory. In concluding his remarks he pointed out that he still held to the glacial origin of intraformational shale-breccias.

Professor W. J. Stephens (1882, pp. 98-106) disagreed on the current-bedding issue, and supported a water-origin, pointing to the even character of the bedding, which suggested sub-aqueous control. Stephens made an ingenious suggestion that was really a compromise in the controversy of "wind or water" origin. In deference to Tenison-Woods' emphasis of the grains of sand being rounded, he put forward the possibility of a great tongue of blown sand being available for discharge by water into a lake where stratification would take place.

Professor Liversidge (1882, p. 106) took the view that the deposit was mainly sub-aqueous in development, and he was totally against the aeolian view. He thought the cementing material was largely argillaceous and felspathic, and not hydrated silica, or hyalite, as earlier workers had suggested.

In regard to consolidation of the sandstone terrain Liversidge was inclined to attribute more to cementation than to pressure by overburden.

For a few years little upon the structure of the sandstone was published, but several palaeontological papers appeared, and in one (1886) Professor Stephens described a *Labyrinthodont* from Cockatoo Island which he assumed was indicative of a warm climate at the time of its existence.

In 1886 and 1887 C. S. Wilkinson contributed several articles on Sydney District geology, and referred the origin of the Hawkesbury Sandstone to a mostly freshwater

environment in a great tidal estuary. He was quite convinced that the sculpture of the Blue Mountain region was due to water agencies.

The first reference to contemporaneously contorted current-bedding appeared in 1887 by T. W. E. David. He described the phenomenon as observed by him at Coogee Bay and suggested the possibility that the lateral thrust necessary for the structure may have been connected with glacial action. He stressed the need for further investigation.

In 1891 H. G. Smith presented one of the earliest mineralogical papers. He described barytes crystals from Marrickville. These measured $\frac{3}{8}$ " by $\frac{1}{16}$ " and were stated as being "in the conglomerate that consists of boulders of shale and ironstone cemented together with hardened sand".

In the same year Baker (1891) exhibited a specimen of barytes to this Society, obtained from a ballast quarry at Gosford, and occurring in the Hawkesbury formation in much the same way as the Marrickville crystals (see also Anderson, 1905).

Two years later David (1893) briefly recorded the same mineral from Fivedock, but this was obviously connected with igneous action. David also noted the occurrence of the mineral from the Pymont Quarries. Although the barium was thought to be derived in these cases from barium-felspar, it is quite normal to have barium in ground waters, and by such agency, without igneous influence, the mineral was no doubt produced.

Again, in 1891, H. G. Smith recorded kaolinite from the sandstone at Marrickville. The mineral was present in crystalline masses, sometimes as plates and sometimes as crystals, showing hexagonal boundaries. The kaolinite constituted the cement of the rock. Smith gave a chemical analysis and his recognition of definite crystals of this mineral as a cementing medium was most important.

A further mineralogical contribution from Smith was his record (1894) of almandine garnets in a conglomeratic phase of the Hawkesbury at Pymont. The mineral was present mostly as chips with indistinct cleavage. His analysis shows the garnet to be an almandine-pyrope mixture.

The year 1896 was marked by the delivery of the Presidential Address before the Royal Society of New South Wales by Professor David, the subject being "Summary of our present knowledge of the Structure and Origin of the Blue Mountains of New South Wales". This was a "milestone" paper as far as Sydney District geology was concerned. It traversed a good deal of the scope of previous investigations upon the Triassic (particularly the Hawkesbury Sandstone) and comprised fairly lengthy quotations from the works of Clarke, Darwin, Tenison-Woods and others. David did not add much information to earlier stratigraphical summaries of the Triassic rocks, but the principal purpose of the paper was to describe the Lapstone Hill monocline and to make some remarks concerning the Continental Shelf. One by-product of the discussion upon the igneous rocks of the Sydney District was his final decision that the included blocks of coal measures in the Euroka Creek Volcanic Neck were Triassic and not Permian.

In 1898, in Curran's "Geology of Sydney and the Blue Mountains", many references to the Hawkesbury Series are made.

In 1899 appeared the detailed log of the Birthday Shaft, Balmain Colliery, as recorded by Dun and Rae. This gives a very full stratigraphy for about 600-625 feet of the Hawkesbury Series. In this interval it is to be noted that only 9 feet of continuous conglomerate is recorded, and that the total of the shale layers in the Hawkesbury Sandstone is about 35 feet, the thickest being 8 feet 4 inches.

It is not proposed to notice, in this summary, the many bores that have pierced Hawkesbury Sandstone. Generally the records as published in the Annual Reports of the New South Wales Mines Department are not helpful stratigraphically. Exceptions comprise the Balmain and Cremorne bores where the compilation of the log was so well done (see *Ann. Rept. Dept. Mines*, 1893; 1907).

So many bores that have been put down in the Sydney District began within the stratigraphical interval of the Hawkesbury Sandstone and the records are frequently too generalized to permit correlation of lithological types in the Hawkesbury succession.

A very helpful summary of information regarding bores in the Counties of Camden and Cumberland was published in 1924 (*Geol. Surv. N.S.W., Min. Res. No. 32*).

In connection with the preparation of three important Memoirs upon our Coalfields (see below) many progress reports appeared in the Annual Reports of the Mines Department. As the separate reports were sometimes superseded and later integrated into Memoirs, no reference will be made here to odd pieces of information concerning the Hawkesbury Sandstone, which appeared from time to time.

In the "Kerosene Shale" Memoir, J. E. Carne (1903) presented an interesting account of the Hawkesbury based upon his experience in the field and upon pre-existing information. He emphasized a noticeable contrast in texture that has come to be well known, mainly that fineness of grain seems to characterize the lower portions of the sandstone, especially in the centre of the Basin, and that coarseness in the components is characteristic of the uppermost beds, especially in the Western Coalfield.

In the Western Coalfield Memoir (1908) the same author treated Triassic stratigraphy in an interesting way, and summarized previous knowledge. Carne stated how he had been impressed by the similarities between the Triassic of the Connecticut Valley and that of New South Wales. He described near the top of the series a persistent shale-band, best seen at Mt. Piddington, where *Thinnfeldia* is abundant.

The Southern Coalfield Memoir (Harper) was published in 1915. Throughout this large work there is a wealth of information about the Triassic rocks, their character, tectonic arrangement and physiographic expression. Harper commented upon the origin of the rocks, but was not able to add any new contribution to the problem.

In 1914, in the Handbook for the British Association for the Advancement of Science Meeting at Sydney, Carne gave a brief account of Triassic stratigraphy, and stated his belief that the Hawkesbury Sandstone suffered erosion before the Wianamatta Shales were deposited. This was a view strongly held by Wilkinson in an earlier period. In 1914 also, the Hawkesbury Series was described by Sussmilch in his "Introduction to the Geology of New South Wales".

Between 1915 and 1931, with the exception of palaeontological work, nothing of note was published, but in the latter year Whitworth (1931) recorded a suite of resistant minerals from specimens of Sydney District sandstones, but it is not clear from his paper whether some minerals from Permian sandstones are not also included. Nevertheless, the suite as given probably represents a fair average qualitative statement for Sydney sandstone.

The minerals noted are:

Haematite	Cassiterite
Limonite	Ilmenite
Garnet	Staurolite
Monazite	Epidote
Magnetite	Hornblende
Zircon	Tourmaline
Rutile	Pyroxenes

Apatite and spinel are also accessories in the sandstone in the writer's experience.

In 1932 David, in his Explanatory Notes to Accompany a New Geological Map of Australia, briefly refers to the Hawkesbury Sandstone and places it in a stratigraphical table. In this year also appeared the Handbook for the Sydney Meeting of the Australian and New Zealand Association for the Advancement of Science, wherein is given a particularly well written account of Triassic geology.

This brings us to the end of the summary of work upon the Hawkesbury Series, but the writer wishes to point out that for the purposes of this address no references have been reviewed here dealing with the Hawkesbury Sandstone as a building or engineering unit. A large number of brief reports and statements about this field of enquiry is to be found in the publications of the New South Wales Mines Department, and well-known books and articles on the building stones of New South Wales refer to the Sydney Sandstone.

EXTENT AND THICKNESS.

In many parts of the Basin the boundaries of the sandstone are very imperfectly known, especially in the north and north-west. Concerning thickness, an approximate figure of 900 feet would appear to express the maximum in the Sydney area.

COMPOSITION, CONSTITUTION AND STRUCTURE OF THE SANDSTONES.

In Table 2 a series of analyses of Hawkesbury Sandstone indicates the variable character of its composition. This variability is bound up largely with the proportions of quartz and clayey material present in different specimens. But the variety of cementing media is also a big factor in causing a rather wide range of chemical composition. No intensive researches have yet been conducted upon the chemical composition of the sandstones and especially upon the cements. It is known from general experience, and occasional determinations by the writer, and many others with whom he has conversed, that the following materials are fairly common as cementing media (excluding the iron oxides and hydrates, which will be referred to later):

Ferrous carbonate (siderite).

Kaolinite.

Undetermined clayey material other than visible kaolinite.

Sericitic material.

Silica.

Partially decomposed felspar.

Chlorite.

TABLE 2.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
SiO ₂	91.44	90.52	81.98	74.28	73.72	68.64	87.50	79.28	79.12	79.66
Al ₂ O ₃	4.41	4.95	9.90	11.59	11.74	16.31	7.41	7.96	8.44	9.43
Fe ₂ O ₃	0.50	0.35	0.30	0.40	4.60	3.90	0.60	1.40	0.70	0.10
FeO	0.18	0.18	2.07	2.79	0.81	0.81	0.09	2.88	3.42	3.00
MgO	0.18	0.17	0.11	0.81	1.08	0.92	0.10	0.41	0.59	0.56
CaO	0.34	abs.	0.15	1.14	0.44	0.68	abs.	0.32	0.14	0.64
Na ₂ O	0.04	0.19	0.18	0.36	1.64	1.08	0.31	0.62	0.66	0.23
K ₂ O	0.60	1.11	1.45	1.75	1.14	1.24	0.36	2.39	2.22	2.16
H ₂ O+	1.57	2.10	8.56	2.94	4.28	5.64	2.96	2.46	1.74	1.52
H ₂ O-	0.25	0.24	1.14	0.80	n.d.	n.d.	0.24			
TiO ₂	0.52	0.30	0.05	0.55	0.22	0.32	0.22	0.52	0.75	0.45
P ₂ O ₅	0.01	0.08	—	—	0.08	0.22	0.05	tr.	tr.	—
MnO	abs.	less	—	tr.	0.02	0.04	tr.	0.02	0.06	—
		0.01								
SO ₃	abs.	abs.	—	0.06	tr.	tr.	0.03	—	—	—
CO ₂	abs.	abs.	—	3.03	—	—	0.04	1.97	2.34	1.94
Organic	abs.	abs.	—	—	tr.	tr.	—	—	—	—
Cl	—	—	—	—	—	—	0.02	tr.	tr.	—
	100.04	100.19	99.89	100.50	99.77	99.80	99.93	100.23	100.18	100.29

I. Kaolinised Sandstone, Botany Brick Works. *Ann. Rept. Dept. Mines, N.S.W.*, 1915, p. 197.

II. Iron-stained Sandstone, Botany Brick Works. *Ann. Rept. Dept. Mines, N.S.W.*, 1915, p. 197.

III. Sandstone, Undercliffe Quarry, Tempe. *Ann. Rept. Dept. Mines, N.S.W.*, 1905, p. 165.

IV. Sandstone, Cataract River. *Ann. Rept. Dept. Mines, N.S.W.*, 1906, p. 182.

V. Sandstone, Por. 15, Par. Picton, Co. Camden. *Ann. Rept. Dept. Mines, N.S.W.*, 1924, p. 105.

VI. Sandstone, Por. 15, Par. Picton, Co. Camden. *Ann. Rept. Dept. Mines, N.S.W.*, 1924, p. 105.

VII. Sandstone, 7 miles east of Mount Werong. *Ann. Rept. Dept. Mines, N.S.W.*, 1914, p. 217.

VIII. Sandstone, Core from Diamond Drill Bore, North Bondi Quarry. *Ann. Rept. Dept. Mines, N.S.W.*, 1922, p. 103.

IX. Sandstone, Core from Diamond Drill Bore, North Bondi Quarry. *Ann. Rept. Dept. Mines, N.S.W.*, 1922, p. 103.

X. Sandstone, Gosford Freestone Quarry. *Ann. Rept. Dept. Mines, N.S.W.*, 1926, p. 104.

Some of these materials are bulk-allogenic constituents, but others seem to have been deposited *in situ*, as, for example, kaolinite and some of the siderite, which no doubt is due to reactions going on in the sediments while wet. The common occurrence of secondary growths of silica (the macroscopic effects of which were so readily observed by the earliest workers) raises the question of the origin of this peripheral addition. A

kind of *regional cementation* due to ground waters is the only major influence that the author can suggest. This would have to operate on a large scale. It is well known, of course, that the Hawkesbury Sandstone becomes case hardened on exposed cliffs and other faces of rock outcrop. This is due to gradual deposition of silica from oozing ground waters that have obtained silica by migration through the zone of weathering. It is possible that slow wholesale solution of silica has gone on through the ages and that peripheral enlargement of sand grains, and/or surface case-hardening, represent a transference of silica from one part of the terrain to other locations.

In the Hawkesbury stratigraphy a series of whitish clay layers is a common occurrence. These are distinct from the grey shaly layers about which something has already been said. The clayey lenses and stratiform deposits appear to be decomposed rock which was largely felspathic in its original condition. Some of these layers of white clay *appear* to be decomposed basic sills, until one examines carefully the constitution and detects sand grains through the "soapy" clay.

In view of the knowledge now available due to the modern mineralogical study of clay materials it is pertinent to enquire as to whether minerals other than kaolinite are present in the Hawkesbury Sandstone. No X-ray analyses have yet been performed, but it will be important for such study to be undertaken. The presence of a considerable amount of an authigenic micaceous substance along the stratification planes of very argillaceous types of sandstones prompts the enquiry as to whether this material may be illite, one of the hydro-micas so well known in ceramic-mineralogy. Mr. Moye suggested independently to the writer the probability that much which was called "authigenic muscovite" may be illite.

A close petrographic study, aided with modern mineralogical techniques, will be needed before the origin and functions of several cementing media are determined. The writer has noticed many times the occurrence of micaceous material, sheaf-like in structure, and forming a good proportion of the sandstone cement. This mineral has not the properties of either muscovite or illite. Then again, some of the chloritic-looking substance in cements appears to have a very pale, almost colourless character, and a refraction different from that of described chlorites. It will be seen, then, that the composition of the sandstones is a subject needing much research.

As regards the determinable constituents excluding cement, apart from quartz, we note the resistant minerals listed above. Also, muscovite is fairly common, although always in very small flakes. The presence of graphite is a matter for some reflection. It may be said that graphite is one of the most characteristic components of the sandstone, and in many places becomes quantitatively considerable. Many finely drawn dark lines in the sandstone provè to be partly made of graphite, and in some current-bedded layers macroscopic graphite becomes so common as to impart a micaceous or semi-adamantine lustre to the rock. The mode of derivation of the graphite from the former organic debris presents a real problem, especially as the rocks have not passed through vicissitudes that would suggest the evolution of graphite from plant remains.

Iron Compounds.

From earliest times of geological knowledge of the sandstone the widespread and frequently abundant occurrence of iron-compounds has been commented upon. The manner of development may be summarized as follows (embracing some recent observations by the writer):

- (a) Crystals and flakes.
- (b) Bands or layers of fairly extensive dimensions.
- (c) Concretionary masses and nodules—
 - (i) Purely syngenetic.
 - (ii) Pene-contemporaneous.
 - (iii) Epigenetic.
- (d) Discontinuous blebs and slabs along current-bedded layers.
- (e) Tubular units.
- (f) Fillings in joints and strata-planes (epigenetic).

(a) In some of the more porous sandstones small crystals of pyrites and flakes of pale-coloured marcasite have been noted in shafts and bores, these eventually changing to haematite. Some jarosite was determined as present in weathered sandstone crusts from Wallacia and also from Oyster Bay.

In a quarry between Earlwood and Bardwell Park haematite occurs in small metallic flakes in a strongly ferruginous sandstone.

(b) The well-known bands of ironstone so prominent on the Blue Mountain Plateau need some study. Many of the occurrences seem to be due to fluctuations in the water table throughout a long period of time, the iron being deposited in much the manner of laterite and oertstein in soils. Climatic cycles would explain some of the features to be noted in the western part of the Hawkesbury Sandstone territory, particularly in cuttings on the Mt. Victoria-Mt. Tomah road. The fantastic shapes assumed by the ironstone, while exciting popular interest, give food for thought to the geologist. Apparently such criteria as texture, permeability, groundwater movement, etc., affect the ultimate form of the deposit.

(c) A wide field of research could be opened up on the concretionary masses of the Hawkesbury. These interesting structures are often seen as solid bodies with vivid brown and red colours, while at other times they are present as earthy brownish units with marked concentric shell structure. Other common modes of occurrence are the beautifully drawn concentric layers of deposition cutting through the sandstone, sometimes in regular curvilinear fashion, and at other times by erratically changing sinuosities.

(i) The purely syngenetic structures are those which have no signs of the bedding having been formed around them, as is the case with epigenetic units which are developed at a stratigraphical junction. The true syngenetic concretions are those which originally were probably made of ferrous carbonate which has altered to some or all of limonite, haematite and turgite.

(ii) Pene-contemporaneous structures are common in the Hawkesbury Sandstone. They are to be found generally associated with shale lenses and fragments of rather small size, along a divisional plane, such as between current-bedded and massive strata. The concretions, generally of limonite, are hydrated forms of earlier anhydrous units. They have been deposited along the sedimentary interface by streams that broke up swampy areas of shaly and peaty environment. In fact, the association of these iron concretions with black carbonaceous shale fragments indicates a genetic relationship. I take the view that these concentrically constructed limonitic masses were originally in the condition of ferrous carbonate. Good examples of these structures can be seen in the large quarry at Undercliffe, at West Arncliffe and in quarries of the Woy Woy district.

(iii) Epigenetic concretionary structures are well known and have only been mentioned here for the sake of completeness. Some excellent ones are known from the Avon Dam area, and they abound in the Sydney Basin. No doubt nuclei of iron compounds have been the starting point for these structures, and rhythmic precipitation, as well as progressive diffusional precipitation may have occurred, somewhat in the manner of the Liesegang Reaction. Giant concretions of this kind have been responsible for the obliteration of original bedding in a terrain, with resulting "pseudo-bedding" making its appearance. Epigenetic concretions have a certain amount of hydration-folding associated with them in the western areas of the Hawkesbury terrain.

(d) Recent observations by the writer in the Katoomba-Mt. Victoria-Mt. Tomah sector have included the study of some interesting blebs and small slabs of ironstone, rich in haematite, in the inclined layers of the current-bedding. These are somewhat different from the epigenetic fillings which are so common in many divisional planes of the Hawkesbury Sandstone. The structures in question are probably to be explained

as due to alteration of ferrous carbonate which was deposited in a carbonaceous-carbonate slurry brought down by the currents operating on a nearby delta lake. Later alteration of the sideritic material has produced the layers of iron oxide. In connection with this hypothesis I would cite the similar relationships for the graphitic and carbonaceous layers to be seen in the current-bedding of the old excavations beside the Oyster Bay Gasometers. There, graphite and coaly films (see later) are found down the current-bedded laminae. The materials of these were undoubtedly contemporaneously deposited.

(e) Along the Mt. Tomah road excellent opportunities exist in the many new cuttings for examining the ferruginous phases of the Hawkesbury Sandstone, since it appears that in the western region of the Basin, a great deal of activity by iron solutions stamped the environment at some stage in the lithological evolution of the Hawkesbury terrain. Thus in this district there are occasionally to be seen tube-like units of turgite and haematite, and occasionally limonite. These are found in thinly bedded and friable white sandstone. The exact mode of development is not yet known.

Other ferruginous bodies in the Hawkesbury are known, and doubtless the reader has observed various things not mentioned in this section. However, it is not intended here to give an exhaustive account of this or any other aspect of Hawkesbury Sandstone geology.

Ripple-Mark in the Hawkesbury Sandstone.

The Hawkesbury Sandstone is in marked contrast with the Narrabeen Sandstones in the matter of development of ripple-mark and cognate structures. It is inaccurate to state that ripple-mark is characteristic of the younger sandstones. On the contrary, it is rather rare. The examples noted by the writer of low-amplitude ripple-mark were all of the current-formed type. However, an interesting occurrence of large-scale ripple-mark was found on the road between Bell and the Mt. Wilson turn-off from the Tomah Road. The ferruginous sandstones here are beautifully rippled by a structure, slightly asymmetric in profile-section, which has a wave-length of about 2 feet 9 inches and an amplitude for the ripples of about 4 inches. A similar deep ripple-mark is to be seen fairly high up on the quarry face at Undercliffe. These structures are not to be confused with broad swellings in the bedding of low-dip current-bedding.

Current-Bedding and Allied Structures.

All observers of the Hawkesbury Sandstone have been impressed by the great display of current-, false- or inclined-bedding. In fact it might be regarded as the most distinctive feature of the whole series, taken through its stratigraphical and areal dimensions. It is not possible nor desirable in an address such as this to enter into a full discussion of the many problems raised by the occurrence of these structures, but I wish to record the variety of types of current-bedding (which structures I have been examining, at intervals, for many years).

I take it as my thesis that, under favourable conditions, the normal and complete current-bedded feature may take one of two *main* structural evolutions:

- (a) There may develop a series of double-curved layers, one segment convex upward and the other concave upward, the latter meeting the basement surface in a much gentler sweeping tangency than the similar feature on the upper surface.
- (b) There may be no curvature of the inclined strata but even, more or less uniformly developed (as regards texture and thickness) layers with a constant inter-dip angle. Seen in section these current-bedded deposits generally have a horizontal floor and upper surface so that the inter-dip angles, being truly alternate, are equal.

In the Hawkesbury terrain examples of the first case are not common—i.e., the full structure is rarely seen. Examples of the second type are very common, but probably the most common of all are the examples of the first type with the upper portion (the topset and foreset beds) eroded away. This is the typical environment of the Hawkes-

bury terrain. There have been endlessly occurring currents to wash away a good deal of previously formed false-bedded material.

The writer has always found it hard to picture the evolution of the second type of structure, but a recent monograph on the environment of the Toroweap Formation of Arizona by McKee (1938) gives good examples of this structure and discusses fully this and other types of cross-bedding. McKee says of the non-curving type (p. 118): "Each bed was built forward across a level surface by a current that deposited rather uniform sloping flat sheets of sand. One layer after another was deposited in identical manner, until finally the characteristic pattern resulted. The level upper surface may have been formed by a planation of the tops of the laminations just developed, but in all probability it was largely constructional, the result of a constant water-level and current velocity during deposition causing concentration of sand on the foreset rather than on the topset surfaces, and keeping the top swept clean to a definite level."

This may be the explanation of much of the Hawkesbury structures, but it is to be noted that the other type of current-bedding represents a fundamentally different hydraulic control.

One is reminded of the value of current-bedding in interpreting the structural positions of sequences in overturned rocks, such as the British and Scandinavian Pre-Cambrian. The point to be made here is that the double-curvature is a primary feature so often destroyed by later current action. It is the recognition of the gentle tangency as the normal condition that has led geologists dealing with inverted rocks to test the tectonic positions of some arenaceous terrains.

Various scour-and-fill relationships are common in the Hawkesbury current-bedded zones. Another common feature is the presence of graded bedding which is really the integration of a large number of concentrations of pebbles and coarse mineral fragments which have come to rest at the foot of the long slopes of inclined strata. This is very well seen in the Mt. Tomah-Bell sections.

Speaking of current-bedding generally one may point out that there is present in the Hawkesbury a kind of "sweeping-current-bedding". This is seen in the Woy Woy, Arncliffe, Undercliffe and North Sydney quarry sections. The layers of the inclined strata are of gentle dip and there is a bowing or curvature which proceeds from end to end of the layers. I suggest the term given above for this structure.

In sections to be noted in railway cuttings and elsewhere in the Leura-Katoomba-Hazelbrook sector, very even and thick current-bedded deposits are the rule. One noteworthy feature of some sections near Leura is that the little milky-quartz pebbles are found strung out through the whole of the deposit, being common on the faces of dipping strata, and not concentrated at the floor zone.

Another feature noted in many places is the production, in uniformly sloping structures, of a compound bank involving the building of several layers of uniform thickness and absolutely constant dip and strike. Such a structure with co-planar layers in successive banks generally needs the absence of any intercalated horizontal strata.

Many current-bedded layers are contemporaneously contorted; this feature will be considered below.

In concluding this section one may point out that a very important set of implications regarding origin of sediment and environment of accumulation arises from the prevalence of the various false-bedded strata.

Gnarled Bedding or Gnarly Structure.

These terms are suggested by McKee for some bedding relationships which he finds in the Toroweap Formation of Arizona. It is not always clear whether this type of structure is wholly due to current action or partly due to slumping.

Gnarly bedding, he says, is "developed by slumping". That this is so is supported by "the wavy indefinite character of some of the cross-laminations in the gnarly beds and also by confused mixtures of massive, featureless sandstone and sandstone containing well-defined cross-lamination patterns".

The writer has observed "gnarly" bedding rarely in the Sydney Basin. Two places of its occurrence are between Oatley and Como, and near Wattamolla, in the National Park.

*Slump-bedding, Intraformational Contortions, Shale-breccias and
Kindred Structures.*

Throughout the sandstone areas there are many occurrences of structures to be brought under this heading. Intraformational shale-breccias in which the fragments of shale are well laminated and angular are common, while just as frequent in occurrence are the shale-breccias in which the fragments have been plastic at the time of accumulation, or have been deformed earlier and carried in angular condition to the site of deposition. Many of these shale-breccias make up considerable thicknesses in the stratigraphical column. They have been briefly recorded in many papers, reports, etc., and in the early days were regarded as glacial in origin. The general assignment of these structures to the scouring effect of storm currents upon a delta mud-lake and subsequent deposition of fragments in a washout elsewhere is to dispose too readily of a very interesting and important subject that needs a careful study.

It is clear that several different types of origin can produce these structures.

Some years ago S. W. Carey and the writer studied the beautiful slump-breccias at Maroubra and Malabar and Little Bay. These are amongst the best in the Sydney Basin, and the area of their development must be measured in square miles. In fact, the occurrence is sufficiently widespread locally to be of academic if not of practical stratigraphical value.

Recently the writer made some more observations in this area, and Messrs. B. P. Webb and P. B. Andrews continued the work and completed a small investigation. A description of this region may now be given.

A zone of brecciated material occurs as a narrow horizon in the Hawkesbury Sandstone and is exposed in the cliff faces in the area. It shows its best development in the section revealed in the cliff face between Long Bay and Maroubra Bay. It may be traced north as far as the north side of Maroubra Bay, where, however, it has thinned out and eventually disappears; and to the south as far as Rosa Gully, where it cuts out, possibly due to faulting. Only one outcrop was seen to the south of this—an isolated outcrop in the low cliff at the back of Little Bay.

The zone consists typically of subangular and often deformed fragments of shale, sandy shale and sandstone in a somewhat sandy matrix. For the most part the fragments have an irregular but rather angular outline. The shale fragments are often folded and sometimes strongly contorted, indicating a semi-plastic condition at the time of brecciation. The fragments show a great variation in size, shale fragments up to 8 feet long being associated with some of only a few inches. The matrix is a soft clayey sandstone, usually grey in colour. In any one place where the zone is developed, there is usually a distinct preponderance of fragments of either a sandy or of a shaly nature.

The thickness of the zone is variable, being about 12 feet where best developed, but thinning out almost entirely in some places. It is occasionally split into two, the upper and lower zones being separated by the typical Hawkesbury Sandstone.

The zone is sometimes represented by undisturbed bands of shale or of soft shaly sandstone, white in colour with numerous very thin parallel bands of shale running through it.

Examination of the bed shows that it was usually formed on a somewhat irregular surface which had suffered a certain amount of erosion before the formation of the brecciated zone. The base of the zone is not always horizontal and sometimes cuts across the underlying beds at a low angle. The top of the zone itself usually shows evidence of contemporaneous erosion, large fragments of shale being sharply truncated at the upper margin of the zone.

The brecciated zone was formed by slumping of sediments and not to tectonic movement along a plane of weakness. The atectonic nature of the zone is indicated by a number of factors:

1. Absence of drag folds.
2. Irregular nature of the folding.
3. Presence of undisturbed shale on the same horizon in places where the brecciated zone is poorly developed.
4. No evidence of relative movement at the junctions with the overlying and underlying beds, combining with the irregular nature of these junctions.
5. Great variation, vertically and laterally, in the composition of the fragments.

The following mode of origin is postulated:

A bed of shaly material was laid down on a contemporaneously eroded surface in the Hawkesbury Sandstones, with good development locally. Slipping of the wet sediments then took place due to overloading or sliding down a gently-sloping surface. The unconsolidated water-saturated beds and the partially consolidated material yielded in different ways; the unconsolidated sediments, being highly plastic, suffered complex slump-folding, the stronger, partially consolidated beds were less intensely folded and suffered brecciation. The larger fragments of shale sometimes show low angle thrust faults of contemporaneous origin. The folded masses of shale were subsequently broken up into irregular fragments showing a certain gradation into the matrix rather than sharp outlines, possibly due to flooding.

Varieties of Slump-Folding.—It would be difficult to select a more intriguing or fascinating aspect of Hawkesbury Sandstone geology than that of the slump-folding and related structures which are fairly commonly developed.

We may divide the structures noted in the present study into five categories, although there is a certain amount of transition between some types.

- (a) In this case, rather simple slump structures are present where current-bedding is well developed. The inclined layers are puckered locally without any complexity of form, as at Bondi. Such simple corrugation is a familiar observation among Sydney geologists.
- (b) In the second group the structure is much more complex, but again frequently affects the current-bedded layers. Irregular contortions, often with sharp V-shaped folds, are assembled in a very disturbed zone. Examples of this type are well known as at Palm Beach (in a boulder of Hawkesbury Sandstone), Bronte, Vacluse, and particularly at several places in The National Park. In this variety we have the typical slump-folding expected in what Rettgers calls "soft rock deformation" (1925).

Close inspection of many quarry faces and other sections has led to recognition of three other types of slump-folding which have not generally been reported and certainly have not been described. These are best listed as—

- (c) Club-like or dumb-bell-like bulging in the bedding.
 - (d) Fine slump-laminae along gently inclined major bedding planes.
 - (e) Complicated, but chiefly parabolically curved structure in current-bedded layers.
- (c) This appears to be due to a gradual shifting of sand on a slip-plane where inhomogeneity of texture and variability of water content in the moving layers have caused a local bulging. This type of structure can be seen on the old excavation-face at the Oyster Bay Gas Works, where it was pointed out to the writer by Mr. E. Hosking. A similar structure was examined at Bondi.
 - (d) Where very extensive, gently sloping current-bedded strata occur, as in several parts of the western Blue Mountains area, there is frequently a very evenly textured, well-bedded and whitish sandstone. Minute slump-structures producing slightly aberrant layers are present. They remind the writer of a similar structure in the varves at Seaham.
 - (e) This, I think, is the most interesting of all. Excellent examples are to be seen in several parts of The National Park, at Waterfall, Undercliffe, Arncliffe, and elsewhere.

The disturbance affects fine current-bedded layers at times, as can be seen on the roadside about $3\frac{1}{2}$ miles from Audley towards Stanwell Park. About $4\frac{1}{2}$ miles from Audley the parabolic type is exposed in outcrops some distance from the road on the eastern side. Here the rocks are coarse and the structure is quite extensive, being about 4 chains in length and 2 to 4 feet in vertical section. The layers are turned northwards so that a vertical section is more or less of parabolic cross-section. The possibility of the parallel parabolic shells being due to iron oxide concretions (now bleached or reduced) was dismissed when the lithology showed, by lines of pebbles, etc., that strata had participated in this deformation.

In seeking to explain this type of slide or slump phenomenon one has pictured the gradual sliding of current-bedded layers leading to a double or S-shaped curve in the erstwhile uniformly dipping strata. Subsequent erosion by fast currents has truncated the structure and left the lower half of the curved strata. It seems that this type of structure is to some extent the result of frictional resistance to movement in the early stage of slumping and partly due to the existence of some overburden of sediment which has partaken in the slipping and later has been eroded away with the upper portion of the curved layers. Beautiful examples of this structure occur in the National Park and also at Neutral Bay, Arncliffe, etc.

Carbonaceous and Coal-like Intercalations.

Apart from actual determinable graphite there are intercalated through the sandstones at various stratigraphical levels and frequently in very widely disseminated fashion, patches, films and lenticular masses of carbonaceous material, some of which has a coaly appearance, while other portions are dull, soft and show some of the features of macerated plant remains.

The proximity of carbonaceous shale beds to the locality of occurrence of much of the intercalations now being considered, suggests an origin for them. It would appear that during the accumulation of sandstone in flood periods, the disturbance of peaty sediments in small lakes on the delta surface has led to eventual sweeping down of carbonaceous debris which has been deposited either in very irregular fashion, or as films on current-bedded stratal planes. Since this method of accumulation seems to fit the occurrence of the carbonaceous blebs, it becomes not infeasible to suggest that the films of graphite found in rhythmically banded sediment may have had their ultimate origin in a similar manner.

Occurrence of Vitrain.—Somewhat distinct from the dull carbonaceous material just discussed are the lenses and irregular accumulations of a brightly lustred and brittle coal which, on the basis of its physical properties, must be described as vitrain. Over many years of observations the writer has noticed this material in widely separated localities. Sometimes the lenses are curved and somewhat sinuous, due to the original dimensions and geometry of the deposited sediment. Frequently the vitrain is granular and so fractured that it is impossible to separate it from the host-sandstone without shattering the whole of it. This appears to be due to the presence of "cleat", the characteristic fracture known in vitrain (see Dulhunty, 1945).

The most common occurrence in the Sydney District is in massive or broadly-horizontal sandstone which has accumulated rapidly, but at Oyster Bay Gas Works the vitrain is found in the current-bedded layers.

Some very fine examples of this phenomenon occurred in the Undercliffe Quarry (most of them having now been excavated), and their relationships there were brought under my notice by Miss Esther Wait, who presented to the University Geological Collection a magnificent specimen, in which the vitrain is about one inch in maximum thickness in a lens eight inches in length. The well-displayed cleat in this specimen is produced by fractures at right angles, and in the field, the counterpart of the fragment collected was investigated by me and found to possess one major cleat direction parallel to a major joint-direction in the sandstone.

In the occurrence of these coaly materials lies an interesting problem, since one usually associates vitrain with a stage in the evolution of coal fairly well advanced,

namely, the sub-bituminous stage (see Dulhunty, loc. cit., p. 137). Chemical and physical tests upon coaly materials in the Hawkesbury Sandstone are urgently needed if we are to elucidate the problems attending the accumulation of the host-sediments.

Calcareous Stalactite and Stalagmite Formations.

What is probably a unique occurrence in the whole of the Hawkesbury Sandstone territory is the development of calcareous decorations in a sandstone cave or rock-shelter on the left bank and at the head of Palona Creek, two-thirds of a mile upstream from its confluence with Port Hacking River in The National Park. Here, in rough country, about 150 feet below the plateau level, a series of stalactites, stalagmites, crudely-formed shawls, and other carbonate masses may be seen attached to normal Hawkesbury Sandstone. A fissure at the back of the cave seems to be the source of supply of the impure limestone.

As no intercalated beds of limestone, pure or otherwise, are known to occur in the Hawkesbury Series, the origin of the calcium carbonate in this cave remains a mystery. It is just possible that a former now eroded mass of Wianamatta calcareous sandstone may have been the ultimate source.

THE ORIGIN OF THE HAWKESBURY SANDSTONE.

No discussion upon the major problems of the Hawkesbury Sandstone would be complete without some mention of the rather hackneyed subject of its general origin.

It will be clear from the foregoing discussion, and especially from the brief historical account of geological investigation, that a great deal of information is yet to be obtained before we can hope to solve this question.

In earlier days, as indicated above, there was considerable interest in the subject of the origin of the sandstone and rather strong controversy developed at times, the issue broadly being a case of *Water versus Wind*, i.e., a sub-aqueous or a sub-aeolian origin. Since the days of the pioneers, most Sydney geologists and many visiting scientists have always had a kind of "background" interest in the origin of the sandstone, while a few have been keenly interested and have turned their attention to the problem as opportunity has offered. However, it may be said that the traditional attitude has been to deplore the paucity of workers in the field of Sedimentary Geology and to express the hope that the future would eventually rectify matters and provide the ideal conditions wherein opportunities would arise for full-scale research upon the Hawkesbury Series, and workers would not be found wanting.

It is not possible in this address to improve matters very much, and much the same kind of sentiments must be expressed, but in addressing himself to this problem the writer would like to outline several points pertinent to the discussion, based on his contemplation of this perennial problem.

(a) From the limited amount of mineralogy done upon the resistant-minerals in the sandstone, very little data regarding provenance is available, and therefore any conclusions to be drawn must be tentative. As a good deal of chemical action has modified the sandstones it is probable that post-depositional processes will need to be very carefully evaluated in any mineralogical approach to the question of derivation of the sandstone.

(b) The traditional conception of a western region of granitic mountains for the distributive province for Hawkesbury sediments has been based upon—

- (i) The abundance of quartz grains and quartz pebbles constituting the rocks, and
- (ii) the general evidence of dip-direction in current-bedded strata.

(It has also been alleged that there is a general coarsening of sediment as one goes westward, but this is rather a fallacious conception, as the most interesting case of increase of grain is in the *upper* beds along the western margin of the Blue Mountain Plateau. Actually in the central part of the Basin much of the sediment is coarser than material from the same stratigraphical levels but geographically closer to the boundaries of the Basin.)

Concerning these criteria (above):

(i) The presence of so much quartz and particularly of so much pebbly vein-quartz, and the notable amount of felspathic and argillaceous material in the sandstone, have naturally led to the naming of a great granitic terrain for an ultimate origin. The difficulties underlying this view are many, but it can be pointed out here that even with the present inadequate knowledge of the geology of our State, we know sufficient about the areal distribution and geological history of the rocks in the postulated circum-Hawkesbury Sandstone region to be able to cast some doubt upon the existence of an immense granitic terrain through a considerable interval of latitude. Alternatively, it must be remembered that over much of the region now lying south-west of the present Triassic Basin there has, since Middle Devonian times, existed tremendous areas of quartz porphyry and quartz felsite in which quartz veins rarely occur or are likely ever to have been present. Further, this Marulan-Wombeyan intrusion invaded non-quartzose rocks, and thus a now-eroded quartzite roof cannot be postulated.

It would appear that only in respect of the central-western margin of the Triassic Basin can we link up the conception of a granitic provenance with the known lithology and probable geological history. Thus the Kanimbla granites undoubtedly had a roof largely constituted of Upper Devonian arenaceous rocks, which would help to supply quartz sand.

(ii) Current-bedding is not an infallible indicator of direction of drainage during the building of the sediments involved, but it is a useful structure in this respect. Certainly there is something to be said for assuming a good deal of transport from the south-west, west and north-west, as reflected in the large number of dips by the inclined bedding across the interval N.E.—E.—S.E. Incidentally, the view has long been established that the inclined bedding was almost entirely sub-aqueously developed.

The presence of so much "herring-bone" structure in the current-bedded masses, raises some difficulties about interpretation of the ancient drainage. A fairly full study of an area near Mt. Victoria, Bell and Mt. Wilson convinced the writer that several distributaries to the delta must have existed in Triassic times, these causing very capriciously changing directions of transport in the delta-margin. Similar environments no doubt could be established for other areas.

(c) The general uniformity of sedimentary history for any locality in the Basin, as testified by the stratigraphical section, erects a baffling difficulty. Thus we have to visualise over about 7,000 square miles a general constancy of conditions during which sediment of the same general lithology, texture, and intraformational peculiarities is spread out partaking of almost identical sedimentational vicissitudes and receiving the same impress of a uniform physiographical environment. Through the vast banks of sand countless tiny pebbles of quartz, well rounded, become strung out like "beads on a thread". One can only imagine that much of the sediment has been gradually moved from zone to zone, more distal in relation to the source-rivers. The remarkable thing to note is that a section of the Hawkesbury at Cowan, Arncliffe, Helensburgh, Woodford, Broughton's Pass or Galston (to mention widely separated areas studied by the writer) displays a general uniformity, and in many minor aspects an identity of character.

(d) The presence of interbedded shale horizons through the sandstone and the nature of their entombed life indicate a recurring environment throughout the delta, conditioned by climate and mechanical controls associated with the contemporary stream activities.

That some of these shale horizons merge into disturbed strata signifies (as described above) the local environmental changes.

(e) While considering the derivation of the Hawkesbury Sandstone it is pertinent to remember that much of the sandstone forming the western cliffs and ramparts to the Blue Mountain Plateau is of Middle Narrabeen age. Between this unit and the Hawkesbury there occur Red Beds indicating the special environment needed for their development. Thus we have to push back in time our mental excursions regarding the origin

of extensive masses of current-bedded glistening quartzose sandstones, marked by an absence of basal conglomerates!

(f) A good deal of concentration is always placed upon the discussion of the western origin of the Hawkesbury Sandstone. The main mechanical difficulty about this is the question of gradual transport of sand and pebbles across the delta with a maintenance of uniformity of sedimentary type. For such a large area of deposition it is reasonable to suppose that a considerable amount of sediment came from *several* supply-zones. Although we are much in the dark about Triassic geography, we can be fairly certain that the Narrabeen Lake was delimited to the north-east by the great wall of the risen and still rising Carboniferous upthrust highlands, which reached much of their height and provided a shoreline in epi-Permian time. The general shape of the Triassic Basin and the postulated boundaries of the Narrabeen Shore make it very unlikely that the eastern margin of either the Narrabeen or Hawkesbury Lakes were at a great distance east of the present coast. Therefore we have the problem of the filling of the eastern side of the Basin by westerly-derived sediment, as there is no sign in the Hawkesbury of a coming in of an easterly phase of sedimentation.

(g) For a Basin so large as the Hawkesbury it is strange that there is so little in the way of facies-changes in the sediments. One has not forgotten that we are not dealing with a marine environment, but as there is such a chemical and lithological variety in the various facies of the Narrabeen succession (cf., for example, the contrast of type in the Upper Narrabeen of Murrurundi and of Avalon), one might have expected some facial variation in the large Hawkesbury area. (It may be that closer study of the life of the period, particularly the non-floral life, may show that considerable physical diversity marked the Basin from place to place, although the textural characters of the rocks are remarkably constant.)

In conclusion, one can only repeat that the problem is an outstanding one that needs much study of convergent evidence. The writer might conveniently mention here that in conversation on this topic Professor Leo A. Cotton pointed out that Professor H. E. Gregory (formerly of Yale) had opined that the Hawkesbury Sandstone was similar to the "High Plains type of deposit in U.S.A.". I have not been able to find out just what that term implies, but in finality would say that a field for fruitful enquiry would be along the lines of studying modern deposits of a continental or piedmont environment where fluvial action was the predominant agent of transport.

STRUCTURE AND PHYSIOGRAPHY.

Over many years the geological structure and the tectonic history of the Sydney region and the nearer highlands have interested the writer, and recently some attempt has been made to integrate observations made over a long period of time, and also to popularize among senior students the many interesting problems in the structural geology. Again, it must be said that, apart from notable exceptions already enumerated, the area under discussion has had a kind of "Cinderella" role in respect of modern geological investigation.

In an earlier period the gradual delineation of the broad structure of the Sydney-Blue Mountains region and the coastal strips north and south of Sydney occupied a long interval of investigation, some of the chief contributors being Clarke, Wilkinson, Tenison-Woods, David, Andrews, Carne and Willan, to give an incomplete list. In many cases a consideration of the tectonics could not be separated from a discussion of the physiography, for these two aspects of Central Eastern New South Wales (as well as of many larger areas) are complementary and genetically interwoven.

It is my purpose in this section of the address to summarize some structural data that have accumulated in my own recent work and in that of some contemporary students and to link the information to the geological history of the Basin.

OBSERVATIONS ON FAULTS AND JOINT SYSTEMS.

For many years all kinds of structural breaks (faults, joints, etc.) and related or associated igneous structures have been examined and details of dip and strike, etc., recorded.

Contributing to this study have been several students of the University and Technical College, the chief workers being Messrs. Andrews, McInnes, Warner and Webb, to whom I am indebted for some information recorded here.

It is clear that a considerable amount of interesting structural data is yet to be gleaned before far-reaching conclusions can be reached about tectonic evolution, but the information at present available points to very intriguing problems in Sydney District geology.

South Coast District.

A. Joints.

In the excellent cliff and rock platform exposures perfect examples of joint systems are available for study, and a considerable number and some variety of faults are present. The measurement of the joint-systems led to the following results:

- (a) *Otford-Bald Hill district.*
Dominant directions N 20° W and W 10° S, in conjugate relationship. Other less important joints present.
- (b) *Bulgo Head.*
N 18° W and N 63° E as dominant directions.
- (c) *Undola Head.*
N 30° W and N 60° E as dominant systems.
- (d) *Coal Cliff.*
Intersection of N 2° E and N 35°-40° E.
- (e) *Clifton-Wombarra.*
Strong N-S direction and less strong E-W.
- (f) *Between Wombarra and Coledale.*
N 30° E, N 64° W and N 18° W.
- (g) *South Coledale.*
Two associated patterns.
(i) N 60° E and N 7° W.
(ii) N 24° E and N 64° W.
- (h) *Long Point to Austinmer.*
Dominant direction N 2° E to N 7° W, cut by one or other of the following conjugate systems: N 40° E and N 65° W.

B. Faults.

A large number of small faults, generally beautifully displayed either stratigraphically or physiographically, are to be seen in the Bald Hill-Otford and Stanwell Park areas. Further south small faults are common, but a large fault is well exposed just south of Coal Cliff.

The majority of the faults dip steeply and are normal, with throws up to a maximum of 12 feet, but two large structures deserve special mention:

- (i) At Bald Hill a fault striking about N. 23° W. cuts through the Narrabeen and Hawkesbury Series and has a throw of 90 feet in a south-westerly direction. This fault shows up very well physiographically, but it appears to pre-date the formation of the plateau.
- (ii) Just south of Coal Cliff on the unstable face of the great cliff so dominantly developed there, is a splendid expression of a fault which strikes perpendicular to the coast (E. 10° N.) and has thrust up the southern side by about 120 feet. The rocks displaced here are Narrabeen Series, but no trace of the fault intersecting the Hawkesbury Sandstone could be found.

Joints in the Long Bay Area.

As typical of the Sydney area, an examination has been made of the Maroubra-Long Bay-Little Bay district. Here the following directions are prominent:

- (a) North-South.
- (b) East-West.
- (c) North-west-South-east.

Groups (a) and (b) form a system of mostly vertical cracks identical with similar systems elsewhere in the Sydney region. Sometimes there is a small hade, but on the whole they are vertical.

The joints in the third direction have been produced independently of (a) and (b) and form a conjugate system due to compression in the manner described by Bucher (1920) in his well-known analysis. At Long Bay the dip on the south-west side is to the N.E. at about 65° and on the north-east side is to the S.W. at about 55°. The intersection of the two sets is along horizontal lines which have directly controlled the injection of the large Long Bay dyke. Apart from this major dyke, others are mostly in the E.W. fractures or in planes whose strike varies a little from this.

Fractures in Other Areas.

From a wide selection of districts much data regarding fracture and fault patterns in the Sydney District is gradually being assembled. The writer has initiated a plan of research which will be spread over some years, devoted to the task of analysing the fracture systems of the Sydney and surrounding regions.

It is not appropriate here to discuss fully the dynamical and geometrical analysis of data cited above, which, however, serve to illustrate the type of investigation which is being conducted in many places. In later work stress and strain diagrams will be employed.

It is quite clear that at least two periods of joint and/or fault formation characterized much of the Sydney Basin, and that probably rotational stresses have not been responsible for the major systems, although *local* stress-conditions may have been characterized by this type of deformation.

As the Sydney region has suffered some compression and been the subject of more than one epeirogenic movement since Cretaceous time, we can expect evidence, in the form of strains, of the broad flexing and warping that accompanied the uplifts of Cainozoic time.

It would appear that frequently joint systems have developed with an orientation more or less identical with an earlier formed set, which had its own distinct tectonic genesis.

The preliminary analysis of many systems observed by the writer and his associates indicates that the main groups are shear joints, conforming to the usual features of shear-patterns. There is, however, a certain amount of tension-jointing, but the clean-cut major fractures indicate shear.

In many places the orientation of the joints was common for both Permian and Triassic rocks, although it was difficult to find a place where a group of joints intersects the junction between the two systems. Nevertheless a very knotty problem arises when the data given in the Southern Coalfield Memoir, together with other information from South Coast Mines, is carefully considered. Indubitable evidence is available of extensive faulting through the Permian Coal Measures, vertical throws amounting to more than 200 feet in places. Invading many of the faults and other fractures is a series of igneous rocks. Contrasted with this environment is the limited amount of intrusion through the Narrabeen Series, and the almost entire absence of faults cutting through the Hawkesbury Sandstone capping which is so well displayed on the plateau 600–800 feet above the displaced Permian measures. It seems inconceivable that all the faults should just die out vertically before the Hawkesbury Sandstone is reached.

An opinion has been expressed at times in the past that a tectonic epoch must have affected the Permian in the South Coast immediately before Narrabeen time, in order to explain the features already outlined. Strongly against this is the stratigraphical evidence in the Balmain Shaft. While overlap is to be seen in the relations of Hawkesbury and Upper Narrabeen, nothing suggesting a break at the base of the Narrabeen is visible at Coal Cliff.

We have here a very important problem, and a searching study of structural features in the rather rugged country of Upper Illawarra is needed.

SOME PHYSIOGRAPHIC PROBLEMS OF THE CUMBERLAND BASIN AND ITS ENVIRONS.

The term Cumberland Basin is used for the structural feature which Willan first established, as shown by the structure details on his Sydney District Map. He noted a complex set of small basins which were named the Penrith, Fairfield, Botany, etc.,

Basins. These are embodied in the trough which is bounded on the west by the Lapstone Hill structure, and limited north and south by the Cattai and Nepean warps, respectively. The eastern limit is the warped sandstone rim, which includes the cliff coastline from Dee Why to Stanwell Park.

In endeavouring to trace the evolution of the present land surface of the Cumberland and surrounding regions, and the relation of that surface to the geological structure, we are faced with the need for unravelling the relationships between the following bodies of data:

- (a) The evidence of the erosion surfaces.
- (b) The sequence of the lavas and intrusive igneous rocks.
- (c) The evidence of the geological structure.
- (d) The data from topographic analysis by the method of altimetric frequency curves.
- (e) The chronology of strand-line movements.
- (f) The distribution of Wianamatta Shale in relation to peneplanation and later warping.

It seems feasible to adopt as a kind of standard working hypothesis the following views concerning the erosion surfaces:

- (i) The oldest discernible surface is the pre-Oligocene one, remnants of which are found rising above the general level of the existing tablelands.
- (ii) The next in age is the Oligo-Miocene surface, which forms the surface of so much of the eastern highlands of New South Wales.
- (iii) Cut below the Oligo-Miocene peneplain is a less well-developed peneplain of Pliocene age. This consists of a number of wide valleys with maximum depth below the Miocene surface of 800 feet.
- (iv) The valley floors of the present cycle of erosion are the result of post-Kosciusko denudation.

In seeking to relate these physiographic time-markers to the sequence of igneous events there has always been some difficulty. It appears that in New South Wales there were three periods of basalt extravasation, and at least two periods of minor basic intrusion. Apart from these episodes the alkaline lavas and intrusions have to be placed. The basalts can be most satisfactorily arranged as follows:

Oldest: Late Cretaceous or Eocene.

Intermediate: Oligocene or possibly early Miocene.

Newest: Late Pliocene.

I would place the Alkaline Complexes earliest of all and perhaps in the Cretaceous. Reasons for this view will be given below.

With this scheme we proceed as follows:

With the assumption that no sediments newer than the Wianamatta Series existed in the Cumberland Basin we may envisage a peneplain at the end of the Cretaceous which cut across the stratification of the shales in the western environs of the Basin. This view is based on a reconnaissance which the writer made at Mt. Tomah recently. Here the old surface cuts obliquely through the slightly dipping Wianamatta stratification.

Basalt was poured out upon this surface, and it would appear that the succeeding uplift was marked by a fairly uniform elevation in the Central part of eastern New South Wales. The erosion which followed carved a somewhat irregular surface on which the middle group basalts were poured. The great peneplanation then ensued.

We now come to the critical question as to whether the Miocene peneplain truncates the Hawkesbury and/or Wianamatta stratification. Several workers with whom the writer has discussed this matter take the view that the warped surface at present constituting much of the highlands is the result of possibly two flexings which affected essentially horizontal strata. That is to say, the physiographic surface is a structural surface, the structural features having been stamped on the areas mainly by the later warpings in Kosciusko time.

W. H. Maze, by his geomorphological studies, using the statistical method of altimetric frequency curves, confirms these views. The writer thinks that while such views are substantially correct, notice must be taken of the evidence of the Wianamatta Series. According to Carne this series was laid down in eroded basins contemporaneously scooped out of the Hawkesbury Sandstone. Most Sydney geologists have seen some evidence of this erosional feature, but over the greater proportion of the Wianamatta territory the structural relations with the Hawkesbury are those of an *apparent* transitional character. The word "apparent" has been used because if small basins were eroded these would have to be filled before the "transitional" strata were deposited on the Hawkesbury surface away from the small basins.

Our next step is to observe that the persistence of outlying patches of Wianamatta Shales at Mt. Tomah and elsewhere in the western Blue Mountains area, and their occurrence in the Mittagong-Moss Vale district point to former widespread distribution. In the absence of a warped floor for the Wianamatta of the Mittagong-Moss Vale areas, one must postulate some faulting to separate these rocks from the Camden-Picton outcrops.

I wish at this stage to suggest consideration of the rather unorthodox hypothesis that the Kosciusko uplift was not responsible wholly for the Lapstone Hill fold and similar flexures. Rather I believe the Lapstone fold to be partly a revealed scarp. My argument for this view turns on the following points:

- (a) Stripping of Wianamatta Shales is going on rapidly from the Kurrajong fold-surface and from the southern Wallacia scarp.
- (b) In the area north of Wallacia, along the longitude of the monocline, there is an area of Wianamatta Shale which conceals the Lapstone structure.

A profile section from "Fairlight" homestead to Mulgoa shows a capping of Wianamatta all the way, and the ground surface truncates the structure. This region, in my opinion, is a key to what happened in post-Miocene time in the Cumberland Basin. That is to say, a good deal of erosion revealed the old flexure which, while not wholly covered, was partly concealed by Wianamatta Shale.

Anyone studying the Camden, Picton and Mt. Gilead areas is impressed with the evidence of post-Miocene erosion. Ridges up to 1,000 feet above sea-level rise well above the general level, and considerable dissection of the valleys has occurred.

To restore the Wianamatta from Camden and the Razorback by extending the present outcrops northward and north-westward would provide a surface which existed prior to Miocene erosion. A corollary of this view is that the monocline is older than the warpings that reflect the physiographic surface, and that the floor of the Cumberland Basin is partly Pliocene in age.

By giving the Wianamatta Shales a much wider distribution and a thicker stratigraphy than usually has been done we obtain a reasonable explanation of the injections of the large laccoliths like Bald Mountain, Stormy Mt., and the Porcupine in the Barigan-Burrembelong district and such structures as "The Gib" and other intrusions of the Mittagong district. With a good cover of Wianamatta Shale existing well beyond the present outcrop, intrusion could be effected.

In the absence of Jurassic or Cretaceous rocks I feel one must postulate a thick Wianamatta Series, otherwise the laccoliths in the Barigan area would have broken out as extrusions.

It is not possible here to discuss Pleistocene strand-lines of our coast, except to stress the point that, assuming the validity of the physiographic evolution given above, the Cumberland Basin would not be flooded by the sea when higher old strand-lines existed. On the hypothesis that the surface of the Cumberland Basin is essentially part of the Miocene penplain, the writer finds difficulty when considering the fluctuations of strand-lines in late Pleistocene and post-Pleistocene time. No fossil evidence of any marine incursions of early Recent time have been found along our Central-Eastern coast.

The presence of lateritic ironstone gravel on low-lying surface portions of the Cumberland Basin recalls the same type of occurrence on the surface of the Pliocene valley floor at Carrick and Towrang, near Goulburn, and also in the Oberon Pliocene

valleys. This raises a challenge to the hypothesis that all the duricrust belongs to one period of formation.

CONCLUDING REMARKS.

To conclude this long discussion of the Sydney Basin:

We have traced the various vicissitudes through which the Triassic rocks have passed. The sedimentational environments have been most varied, and largely rhythmic in the case of the Narrabeen. In Hawkesbury time a puzzling physiographical setting attended the gradual building of the sandstone deposits, and they were derived from a land, the place and geological character of which still make something of an enigma.

After accumulation of very thick Wianamatta Shales over an area much greater than the present outcrop, some folding occurred in pre-Miocene time. The Triassic rocks had to endure various bevellings and were covered by basalts and invaded by intrusives, the remarkable volcanic necks of the Cumberland Basin being associated with the early bulging which gave the Lapstone fold its general embryonic form. Intensification of this early flexing was effected by the Kosciusko uplift and extensive erosion in late Pliocene and Pleistocene time has removed a great amount of the Upper Wianamatta.

Reiterating the earlier statement of the purpose of this address, I hope that some of the physiographic problems of the Sydney District raised here will grip the imagination of younger workers and prompt them to attempt to unravel the romantic geological history since Triassic time.

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The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 29th February, 1948, 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.

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

President: Lilian Fraser, D.Sc.

Members of Council: Ida A. Brown, D.Sc., Lilian Fraser, D.Sc., Professor J. Macdonald Holmes, B.Sc., Ph.D., F.R.G.S., F.R.S.G.S., 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,

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.
BALANCE SHEET at 29th February, 1948.

	£	s.	d.	£	s.	d.
LIABILITIES.						
Accumulated Funds—						
Amount bequeathed by Sir William Macleay	35,000	0	0			
Surplus Income Capitalized	17,035	14	10			
	£52,035 14 10					
ASSETS.						
Fixed Assets—						
Commonwealth Loans, at cost .. .	29,850	0	0			
Debtures:						
Metropolitan Water, Sewerage and Drainage Board, at cost .. .	5,425	19	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	12,950	0	0			
	51,403 14 9					
Current Assets—						
Commonwealth Savings Bank .. .	319	1	6			
Commercial Banking Company of Sydney Ltd.	312	18	7			
	632 0 1					
	£52,035 14 10					

INCOME ACCOUNT. Year Ended 29th February, 1948.

	£	s.	d.	£	s.	d.
To Salaries of Linnean Macleay Fellows	278	4	1			
„ Balance, being Surplus Income transferred to General Account	397	2	0			
„ Capital Account	1,321	15	11			
	£1,997 2 0					
By Interest				1,997	2	0
				£1,997 2 0		

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1948, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1948, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1948.

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

3rd March, 1948.
A. B. WALKOM,
Hon. Treasurer.

BACTERIOLOGY ACCOUNT.
BALANCE SHEET at 29th February, 1948.

	£	s.	d.	£	s.	d.
LIABILITIES.			ASSETS.			
<u>Accumulated Funds—</u>			<u>Fixed Assets—</u>			
Amount bequeathed by Sir William Macleay	12,000	0	0	Commonwealth Loans, at cost	16,320	0 0
Accumulated Income Capitalized	3,820	0	0	<u>Current Assets—</u>		
	15,820	0	0	Commercial Banking Company of Sydney Ltd.	253	5 4
Income Account at 29th February, 1948	1,588	9	6	Commonwealth Savings Bank	835	4 2
	£17,408	9	6		£17,408	9 6

INCOME ACCOUNT. Year Ended 29th February, 1948.

	£	s.	d.	£	s.	d.
To Salary	500	0	0	By Balance from 1946-47	1,449	6 1
" Expenses	1	2	2	" Interest	640	5 7
" Balance to 1948-49	1,588	9	6		£2,089	11 8
	£2,089	11	8			

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1948, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1948, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1948.

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

A. B. WALKOM,
 Hon. Treasurer.
 3rd March, 1948.

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

31st MARCH, 1948.

Dr. Lilian Fraser, President, in the Chair.

Donations and Exchanges received since the previous Monthly Meeting (26th November, 1947), amounting to 32 Volumes, 634 Parts or Numbers, 16 Bulletins, 2 Reports and 4 Pamphlets, total 688, have been added to the Library.

PAPERS READ.

1. Cytological Studies in the Myrtaceae. II. Chromosome Numbers in the Leptospermoideae and Myrtoideae. By S. Smith-White.
 2. A Survey of Chromosome Numbers in the Epacridaceae. By S. Smith-White.
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ORDINARY MONTHLY MEETING.

28th APRIL, 1948.

Dr. Lilian Fraser, President, occupied the Chair.

The President announced that the Council had elected Dr. A. B. Walkom to be Honorary Treasurer and Dr. W. R. Browne, Dr. Ida A. Brown, Mr. A. R. Woodhill and Dr. G. D. Osborne to be Vice-Presidents for the Session 1948-49.

The President referred to the death of Mr. Rowland E. Turner of Cape Town, South Africa, who had been a member of the Society since 1904.

The following were elected Ordinary Members of the Society: Miss Beverley I. Anderson, Miss Greta Baddams, B.A., B.Sc., Miss Judith H. Balmain, Mr. L. C. Birch, B.Ag.Sc., M.Sc., Miss Daphne C. Davison, B.Sc., Mr. D. P. Drover, Mr. E. H. M. Ealey, Miss Judith A. Fraser, Mr. W. Joklik, Mr. T. B. Kiely, Miss Audrey Ludvigsen, Dr. N. W. G. Macintosh, Miss Elizabeth N. Marks, M.Sc., Father J. J. McAreavey, S.J., Captain J. D. McComish, F.R.G.S., Dr. H. S. McKee, B.A., Miss A. Adele Millerd, B.Sc., Mr. A. F. L. O'Farrell, A.R.C.Sc., B.Sc., F.R.E.S., Miss Anne Stokes, B.Sc.

Donations and Exchanges received since the previous Monthly Meeting (31st March, 1948), amounting to 10 Volumes, 129 Parts or Numbers, 6 Bulletins and 10 Pamphlets, total 155, have been added to the Library.

PAPERS READ.

1. Australasian Ceratopogonidae (Diptera, Nematocera). Part V. The *Palpomylia* Group of Genera. By D. J. Lee, B.Sc.
2. Life-history of an Australian Crustacean, *Acetes australis* (Decapoda, tribe Penaeidae). By Muriel C. Morris, B.Sc.

LIFE-HISTORY OF AN AUSTRALIAN CRUSTACEAN, *ACETES AUSTRALIS*
(DECAPODA, TRIBE PENAEIDAE).

By MURIEL C. MORRIS, B.Sc.

(Seventy-three Text-figures.)

[Read 28th April, 1948.]

INTRODUCTION.

The genus *Acetes* was first described by Milne Edwards in 1830 (*A. indicus*), whilst the Australian species, *A. australis*, referred to in this paper was first described by Colefax in 1940.

Since the various stages in its life-history occur together with the young of one at least of our commercial prawns, it has been considered important to make a detailed study of its larvae not only for the intrinsic value of the knowledge obtained, but also because of its bearing on general faunistic studies.

The adult, as well as the larval stages, is typically planktonic, occurring particularly in estuarine waters and coastal lakes rarely beyond the influence of tidal effects (Kemp finds the same for the Indian waters, 1917). All the adults obtained in the course of this research came from the Tuggerah Lakes: some from Tuggerah Lake itself at a point about three miles from the entrance of the lake to the sea, and others from the middle of the three lakes, Budgewoi Lake, at a point about seven miles from the sea, at both of which points there are no tidal effects.

There is always a possibility that estuarine species of Crustacea may pass out to sea to breed as is the case in several of the species of Penaeid prawns which have been investigated. It seems almost certain, however, that the adult *Acetes* found in Budgewoi Lake do not go to sea to breed, but breed in the lake, and all stages captured were caught in the lake itself. It would be impossible for any stages younger than those taken in the lakes to travel from the sea in the time and under the conditions prevailing against the effects of wind and tide to Budgewoi Lake. Again, the fact that adults with mature gonads were taken in the lake further supports this theory.

PREVIOUS WORK ON THE LARVAE OF GENUS ACETES.

The development of the genus *Acetes* has already attracted attention in America, India and Japan, the most detailed description being that given by Menon (1933) for the Indian species *A. erythraeus*.

The work carried out by Brooks (1882) on the development through a few stages of an American species of *Acetes* seems to have been the first attempt at following out the sequence of stages in the development of the Genus. The stages he described correspond to the Third Protozoa, Mysis, First Mastigopus and to one intermediate between Stage VIII and Stage IX of *A. australis*. Brooks thought it quite likely that the larva referred to by Dohrn (*Zeit. f. Wiss. Zool.*, xxi, 1871, Plates 29 and 30, figs. 62-7) and Claus ("Crustacean System", Taf. iv, figs. 2-7) might be an earlier stage than any he had found of a closely related species. In point of fact, it agrees closely with the First Protozoa of *A. erythraeus* and *A. australis*.

Müller, in his "Facts for Darwin", also refers to two *Acetes* larvae—an early Mysis stage and one intermediate between Stages VIII and IX of *A. australis*.

Apart from these descriptions, no other detailed work dealing with the life history of any member of this genus has been found. Colefax (1940), however, refers to the description of the larval development of a species of *Acetes* by Soyejima (*Suisan Gakkwai Ho*, iv, 1926, p. 15), but unfortunately this paper could not be obtained.

COLLECTION OF MATERIAL.

As the adult female of *A. australis* sheds her eggs straight into the water and does not carry them attached to her pleopods, it is natural to expect a long sequence of larval stages. Actually Nauplii, Protozoaeae, Mysis, Post-Larval and Young Adult stages are found—all of which are typically members of the plankton and can be collected by the usual methods.

Catches were made on Budgewoi Lake between February and December, 1946, mostly at night, by hauling nets of various meshes and at varying depths from a boat. They were preserved in a dilute formalin solution on the spot and observed later at the Zoology Department, Sydney University.

Considerable difficulty in obtaining plankton has, however, been experienced in these lakes during the last few years owing to the prevalence of Ctenophores, which are caught in the nets and break up coating the inner surface with gelatinous matter and preventing adequate filtration.

As the duration of the stages is fairly short the chance of "missing" some of them was considerable, especially as it was only possible to make catches every four to six weeks. On the other hand *A. australis* appears to breed practically the whole year round, and so the possibility of getting all the stages was greater than if there had only been a restricted breeding season.

DESCRIPTION OF THE LARVAL AND POST-LARVAL STAGES OF ACETES AUSTRALIS.

The earliest certain stage obtained was the First Protozoa stage, 0.35 mm. in length (Text-figs. 1-1a). It corresponds definitely to Menon's Protozoa I of *A. erythraeus* (Menon, 1933).

No Nauplii or egg-stages of *A. australis* have yet been obtained. This seems rather strange when one considers the large number of First Protozoae captured. It might be explained by assuming that the very early stages, i.e., eggs and nauplii, are demersal, or float very near the bottom, and so would not be taken by the usual methods. It should be noted that although the change from Third Protozoa to Mysis is a radical one, almost suggesting that at least one other stage normally intervenes, only one Mysis stage was described by Menon (1933), and a maximum of two Acanthosoma stages normally occur in other Sergestids. In any case, Brooks (1882) actually watched the metamorphosis from his Protozoa stage to his Mysis stage, which correspond with the Third Protozoa and Mysis respectively in *A. australis*.

In view of the fact that each stage in the life history of *A. australis* closely resembles the corresponding stage in *A. erythraeus*, it is felt that it would be superfluous to describe in detail the appendages of each stage which have already been so fully described by Menon (1933). The appendages are figured, and attention will be drawn to points of difference between the species where they occur.

FIRST PROTOZOEAE—STAGE I. (Text-figs. 1-1a.)

Length from base of rostrum to end of sixth abdominal segment is 0.35 mm. The carapace in *A. australis* is decidedly longer than it is broad, whereas in *A. erythraeus* it is broader than it is long.

The antennule (Text-fig. 2), antenna (Text-fig. 3) and mandible (Text-fig. 4) agree very closely with the corresponding appendages in *A. erythraeus*—except for the lack of a seta on the distal inner margin of the sixth segment of the antennal endopodite—a fact to be noted, since it does not appear in the subsequent stages. The spine occurring on the ventral face of the labrum is considerably smaller than that of *A. erythraeus*, and it does not project beyond the anterior border of the carapace.

The second maxilla (Text-figs. 6-6a), which closely resembles the corresponding appendages in *A. erythraeus*, undergoes no important change until the Mysis stage.

In the case of the first maxilla (Text-figs. 5-5a), first (Text-figs. 7-7a) and second (Text-figs. 8-8a) maxillipedes, the only important difference from *A. erythraeus* seems to be in the number of setae on the endopodites. The presence of one and not two setae on the second endopodite segments in the case of the first and second maxillipedes of

A. australis and one instead of three on the first endopodite segment in the case of the first maxilla may be an artifact. The number shown in the figures was found on all the specimens caught, but in the next stage the increased number of setae was present. It might, however, be noted that the third maxillipede is still non-setous in *A. australis*,



Text-figs. 1 to 8a. First Protozoa—Stage I.

1. First Protozoa $\times 126$. 1a. First Protozoa $\times 19$. 2. Antennule $\times 84$. 3. Antenna $\times 84$. 4. Mandible $\times 84$. 5. First Maxilla $\times 168$. 5a. First Maxilla $\times 84$. 6. Second Maxilla $\times 168$. 6a. Second Maxilla $\times 84$. 7. First Maxillipede $\times 168$. 7a. First Maxillipede $\times 84$. 8. Second Maxillipede $\times 168$. 8a. Second Maxillipede $\times 84$.

whereas it bears two terminal setae in *A. erythraeus*. Whilst only three thoracic segments can be distinguished behind the third maxillipede in *A. australis*, four are distinct in *A. erythraeus*.

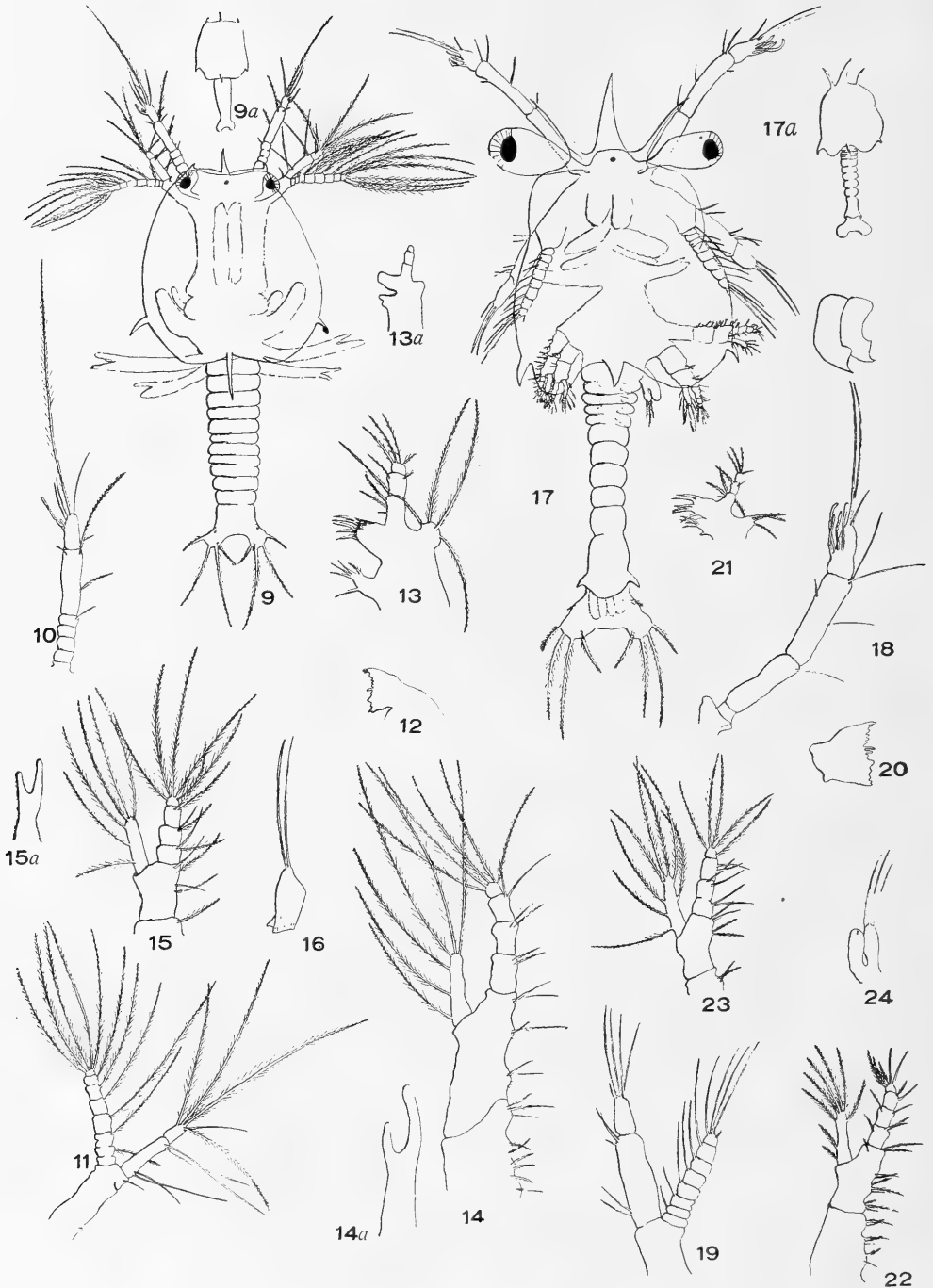
The unsegmented abdomen and widely forked telson closely resemble the corresponding structures in *A. erythraeus*.

SECOND PROTOZOEAE—STAGE II. (Text-figs. 9–9a.)

Length from base of rostrum to end of sixth abdominal segment is 0.7 mm.

The carapace now bears a rostrum as well as the median and paired anterior and lateral spines. The anterior spines are no longer forked in *A. australis*, whereas the forks persist in *A. erythraeus* until the beginning of Third Protozoa Stage.

As will be noted from the figures, the form of the antennule (Text-fig. 10) and antenna (Text-fig. 11) has not changed, except for the acquisition of a pair of aesthetes on the outer margin of the seventh segment of the antennule. Menon refers to a similar occurrence in *A. erythraeus*. It might be noted, however, that the seta on the distal



Text-figs. 9 to 16. Second Protozoa—Stage II. Text-figs. 17 to 24. Third Protozoa—Stage III.

9. Second Protozoa $\times 63$. 9a. Second Protozoa $\times 19$. 10. Antennule $\times 84$. 11. Antenna $\times 84$. 12. Mandible $\times 84$. 13. First Maxilla $\times 168$. 13a. First Maxilla $\times 84$. 14. First Maxillipede $\times 168$. 14a. First Maxillipede $\times 84$. 15. Second Maxillipede $\times 168$. 15a. Second Maxillipede $\times 84$. 16. Third Maxillipede $\times 84$. 17. Third Protozoa $\times 63$. 17a. Third Protozoa $\times 19$. 18. Antennule $\times 84$. 19. Antenna $\times 84$. 20. Mandible $\times 84$. 21. First Maxilla $\times 84$. 22. First Maxillipede $\times 84$. 23. Second Maxillipede $\times 84$. 24. Third Maxillipede $\times 84$.

inner margin of the fourth endopodite segment of the antenna has disappeared in *A. australis*, but is still present in *A. erythraeus*.

The mandible (Text-fig. 12), which now bears twelve–thirteen teeth characteristically arranged on its median border, differs from the corresponding appendage of *A. erythraeus* in having serrations on the dorsal side of the seventh and not on the fourth tooth.

The first maxilla (Text-figs. 13–13*a*) and first (Text-figs. 14–14*a*) and second (Text-figs. 15–15*a*) maxillipedes have undergone no important structural change except for an increase in the number of setae on the masticatory lobes of the first maxilla and the definite division of the first maxillipede protopodite into two segments. As noted above, the endopodites of the first maxilla and first and second maxillipedes now bear the increased number of setae.

The third maxillipede (Text-fig. 16) now bears two terminal setae. Behind the third maxillipedes there are four distinct thoracic segments as in *A. erythraeus*.

The abdomen, now five segmented, and the telson, agree with Menon's description of *A. erythraeus*.

THIRD PROTOZOEAL STAGE—STAGE III. (Text-figs. 17–17*a*.)

Length from base of rostrum to end of sixth abdominal segment is 0.92 mm.

The tri-segmented condition of the antennule (Text-fig. 18) in both *A. australis* and *A. erythraeus* has resulted from the coalescence of the first five segments of the previous stage.

The antenna (Text-fig. 19) now differs from the corresponding appendage in *A. erythraeus*, not only in lacking the setae on the distal inner margin of the fourth and sixth endopodite segments, but in possessing an extra seta on the outer margin of the proximal exopodite segment.

It should be noted that the two pointed teeth (seventh and eighth) on the toothed edge of the mandible (Text-fig. 20) do not bear the dorsal serrations referred to by Menon. As is the case with *A. erythraeus*, the hairy pad, which Brooks (1882) refers to in his Protozoa stage (Plate ix, fig. 80) as occurring on the posterior surface of the mandible, is absent.

As will be seen from the figure (Text-fig. 21), the only change in the first maxilla is an increase from five to six in the number of setae on the distal lobe of the protopodite. A similar increase in the number of setae on the protopodite occurs in *A. erythraeus*, the proximal segment bearing six, whilst the distal segment bears seven. This difference in the setae on the protopodite constitutes the only difference between the first maxillae of the two species at this stage.

The increase in the number of plumose setae on the exopodites of both the first (Text-fig. 22) and second (Text-fig. 23) maxillipedes from six to eight and also the acquisition of another seta on the coxopodite of the second maxillipede, mean that these appendages exactly resemble the corresponding appendages in *A. erythraeus*. Up to this stage, the coxopodite of second maxillipede has borne one less seta in *A. australis* than in *A. erythraeus*.

The form of the third maxillipedes (Text-fig. 24) buds of the four pairs of paraeopods, and the abdomen, with its ventro-lateral spines and buds of the uropods, is the same as in *A. erythraeus*, although Menon states that at this stage he could make out the buds of the pelopods with difficulty.

MYSIS STAGE—STAGE IV. (Text-fig. 25.)

Length from base of rostrum to end of sixth abdominal segment is 1.5 mm.

At this stage the shape of the body has changed entirely, due mainly to the lateral compression of the carapace. Its posterior border is concave and the posterior angles rounded. All the spinous processes have gone, except the rostrum which is short and bears a tooth at its base. There are a pair of sub-orbital spines at the anterior angle and a pair of supra-orbital spines above the eyes. These last-mentioned spines do not appear until the next stage in *A. erythraeus*.

The considerable changes in the mouth-parts and thoracic appendages and the appearance of the abdominal appendages at this stage should also be noted. It is

interesting to note that, although the mouth-parts have changed considerably, they lag behind those of *A. erythraeus* in their assumption of the adult form.

It would appear that in both *A. australis* and *A. erythraeus*, the number of aesthetes on the antennule (Text-fig. 26), which now consists of a three-segmented peduncle and two flagellae, has decreased to two. In the following stages there is a gradual increase in the number of aesthetes until finally, in the adult, the inner flagellum is thickly beset with aesthetes. The swelling referred to by Menon as occurring at the base of the first peduncular segment is not present in this stage of *A. australis*, whilst the outer flagellum is still unjointed in *A. australis* but faintly segmented in *A. erythraeus*.

As will be seen from Text-fig. 27, the antenna has changed quite considerably—the flagellum being homologous with the endopodite of the previous stage, whilst the scale is homologous with the exopodite. A similar change was observed by Menon. The number of setae occurring on the scale increases gradually in the following stages and throughout agrees closely with the number occurring in the corresponding stages of *A. erythraeus*. Apart from an increase in size, number of segments in flagellum and setae on scale, the antenna undergoes no further change in the stages described.

It should be noted that the labral spine (Text-fig. 28) is still present at this stage in *A. australis*, although it is missing in *A. erythraeus*, and persists up to the end of Stage V.

As in *A. erythraeus*, the masticatory lobes of the first maxilla (Text-fig. 29) are no longer armed with setae but with teeth. The endopodite has disappeared in both species, but the remains of the exopodite, bearing four setae, still persists in *A. australis*.

The change in the second maxilla (Text-fig. 30) is not as radical as in *A. erythraeus*. For instance, the prominences on the protopodite still persist, the endopodite is still faintly jointed and setous; whilst in *A. erythraeus*, all the protopodite prominences except one have disappeared, and the endopodite has completely disappeared. It should be noted that the exopodite of the last stage is already expanding to form the "scaphognathite" so well developed in the adult. The number of setae occurring on the "scaphognathite" increases gradually in the following stages, but is always less than in *A. erythraeus*.

Once again the change in the form of the first maxillipede (Text-fig. 31) is not as radical as in *A. erythraeus*—for instance, the endopodite still persists, whereas in *A. erythraeus* at this stage it has completely disappeared.

Both the second (Text-fig. 32) and third (Text-fig. 33) maxillipedes are gradually assuming the adult form, and in this connection it is interesting to note that the five-segmented endopodite of the third maxillipede is already longer than the endopodite of the second maxillipede.

As in *A. erythraeus*, the small biramous paraeopods of the last stage have changed into well-developed forwardly-directed legs consisting of a five-segmented chelate endopodite and an unjointed exopodite—the fourth, of course, lacks the endopodite.

The form of the abdomen, with its ventro-lateral spines on the first five segments and its dorsal spine on the sixth segment, and with the three pairs of uniramous pleopods, is the same as in *A. erythraeus*. The uropods (Text-fig. 34) differ from the corresponding appendages in *A. erythraeus* in the number of setae borne on the rami. The only changes in the uropods observed in the following stages are an increase in size and an increase in the number of setae borne on the rami.

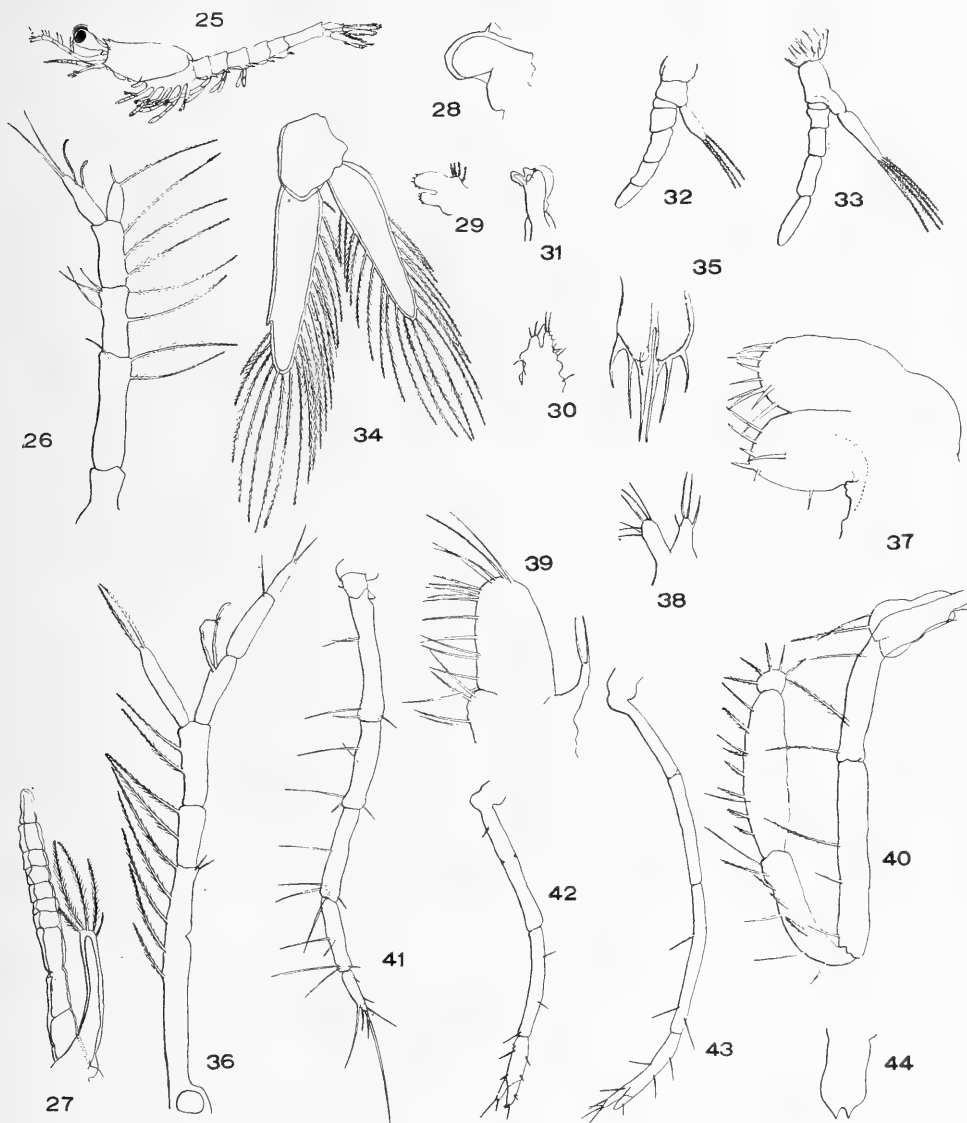
The form of the telson (Text-fig. 35) is very similar to that observed by Menon in the First Mastigopus of *A. erythraeus*. The six pairs of setae have shortened into spines, of which there are now only four pairs. In *A. erythraeus* the setae have shortened into spines, of which there are still six pairs.

FIRST MASTIGOPUS STAGE—STAGE V.

Length from base of rostrum to end of sixth abdominal segment is 1.7 mm. This may be regarded as the first Post-Larval Stage, as the pleopods, and not the more anterior appendages, are used in propulsion. Gurney (1942), in describing some of

the larval forms of the Sergestidae, describes this as the first Post-Larval Stage, but strangely enough, he states that the spines on the carapace and abdomen of the larval stages disappear on the assumption of the Mastigopus stage. It was observed that in both *A. australis* and *A. erythraeus*, these spines disappeared after the Third Protozoeta Stage.

The swelling, referred to above, as occurring in the Mysis stage of *A. erythraeus*, is now present on the base of the first peduncular segment of the antennule (Text-fig. 36)



Text-figs. 25 to 35. Mysis—Stage IV. Text-figs. 36 to 44. First Mastigopus—Stage V.

25. Mysis $\times 19$. 26. Antennule $\times 84$. 27. Antenna $\times 84$. 28. Labrum $\times 84$. 29. First Maxilla $\times 84$. 30. Second Maxilla $\times 84$. 31. First Maxillipede $\times 84$. 32. Second Maxillipede $\times 84$. 33. Third Maxillipede $\times 84$. 34. Uropods $\times 84$. 35. Telson $\times 84$. 36. Antennule $\times 99$ approx. 37. First Maxilla $\times 190$ approx. 38. Second Maxilla $\times 63$ approx. 39. First Maxillipede $\times 190$ approx. 40. Second Maxillipede $\times 230$ approx. 41. Third Maxillipede $\times 110$ approx. 42. First thoracic $\times 23$ approx. 43. Second thoracic $\times 23$ approx. 44. Telson $\times 80$ approx.

and contains a statocyst. It should also be noted that the outer flagellum is now three-segmented—the segmentation having occurred in the Mysis stage of *A. erythraeus*.

With the loss of the exopodite, the first maxilla (Text-fig. 37) resembles the corresponding appendage in *A. erythraeus*—except in the number of setae occurring on the endites. The only further change in this appendage in the stages studied is an increase in the number of setae on the endites, there being usually fewer than in the corresponding stage of *A. erythraeus*.

As in *A. erythraeus* the second maxilla (Text-fig. 38) has now lost its protopodite prominences and endopodite whilst the protopodite has expanded to form an endite bearing six plumose setae. Thus it now resembles the corresponding appendage in *A. erythraeus*.

With the loss of the endopodite and the acquisition once again of setae the first maxillipede (Text-fig. 39) is assuming the adult form. The number of setae on the protopodite increases throughout the following stages until the hairy appearance of the adult appendage is attained. The epipodite which Menon referred to as being present in this stage of *A. erythraeus* occurred in some of the specimens dissected, but not all.

The second maxillipede (Text-fig. 40) has assumed adult characters with the loss of the exopodite and the assumption of the V-shaped form. The basipodite of the protopodite has fused with the ischiopodite of the endopodite, so that altogether there are now only six segments. It should be noted that the exopodite persists in *A. erythraeus* as a small, unarmed vestige until the next stage. In the following stages observed in *A. australis* there is no important change in the second maxillipede and no sign at any stage of the epipodite which occurs in Stage VII of *A. erythraeus*.

The exopodite, which persists until the next stage in *A. erythraeus*, has been lost from the third maxillipede (Text-fig. 41), which is now a long, slender appendage which persists in its present form in all the following stages.

There are now only three pairs of thoracic legs, the uniramous fourth pair having been lost. This difference is an important one as it affords a quick means of distinction between a Mysis and a Mastigopus stage. The appendages are now uniramous (first thoracic leg, Text-fig. 42; second thoracic leg, Text-fig. 43), the unjointed exopodite having been lost. In *A. erythraeus* the exopodites do not disappear until the next stage. It is interesting to note that the suture between the ischium and the merus of the endopodite of all the legs is now indistinct and remains so until at least Stage X. This seems rather strange when one realizes that the same suture was quite distinct in previous stages. The thoracic appendages undergo no further important changes in the following stages.

The pleopods differ from the corresponding structures in *A. erythraeus* only in the number of setae borne on the second exopodites. (The acquisition of setae on the pleopods affords a useful means of distinguishing quickly between a Mysis and a Mastigopus Stage.)

The telson (Text-fig. 44) differs quite markedly from the corresponding structure in *A. erythraeus*, which now bears two pairs of spines. (A further description of the development of the telson in the Post-Larval stages of *A. australis* is given at the end of the descriptions of the various stages.)

STAGE VI. (Text-fig. 45.)

Length from base of rostrum to end of sixth abdominal segment is 1.9 mm.

The changes characteristic of this stage observed in the antennule (Text-fig. 46)—acquisition of two setae on the statocyst swelling, increase in number of segments in outer flagellum—were referred to by Menon. The number of segments in the outer flagellum seems, however, to be less than in *A. erythraeus* in all the stages observed. The inner flagellum, which is still unjointed in *A. erythraeus*, is two-segmented in *A. australis*.

The mandible (Text-fig. 47) persists in the form figured in all the following stages. It should be noted that in some specimens there were two ventral teeth as in *A. erythraeus*.

An epipodite is now definitely present on the protopodite of the first maxilliped (Text-fig. 48). In the following stages it increases in size, becoming a flat, oval structure.

In both *A. erythraeus* and *A. australis* the third (Text-fig. 49) and fourth (Text-fig. 50) pleopods are now biramous whilst the rudiments of the fourth pair have increased in size. Once again the number of setae on the exopodites of pleopods one, two and three differs in the two species.

STAGE VII. (Text-fig. 51.)

Length from base of rostrum to end of sixth abdominal segment is 2.2 mm.

This stage is actually a stage between Menon's VI and VII. The mouth-parts are the only parts which lag behind in development; but this retardation of development seems to be constant enough to warrant the formation of another stage.

There is no trace of the small spine referred to by Menon as occurring on the outer distal angle of the basal swelling on the first peduncular segment of the antennule (Text-fig. 52)—one of the reasons why this should be regarded as an extra stage.

In this stage the labrum (Text-fig. 53) acquires a pair of fine spines on the ventral surface and persists in this form in all the following stages. Menon makes no reference to these spines.

The single endite of the second maxilla (Text-fig. 54) bears six to seven terminal setae whereas eight occur in Stage VII of *A. erythraeus*, whilst there is no trace of the seta referred to in Stage VII by Menon as occurring on the middle of the proximal border, nor of the rudimentary palp on the outer margin of the base of the endite. These differences in the second maxilla constitute another reason for regarding this as an earlier stage than Stage VII of *A. erythraeus*.

The ventro-lateral spines of the first five abdominal segments have now become flattened into plates from which the pleura of the adult tegmenta are formed. Menon makes no further reference to the abdominal spines after he first describes them.

It is interesting to note that in Stage VII of *A. erythraeus* the fifth pair of pleopods (Text-fig. 57) is uniramous (third pleopods, Text-fig. 55; fourth pleopods, Text-fig. 56). In the next stage of *A. australis* to be described—i.e., the Fourth Mastigopus—which corresponds with Menon's Stage VII, the fifth pair of pleopods is biramous, and so in this respect the fourth Mastigopus Stage is more highly developed than the corresponding stage of *A. erythraeus*. In Stage VII (Third Mastigopus of *A. australis*) the number of setae on the exopodites is, as is to be expected, less than in Stage VII of *A. erythraeus*. However, it will be noticed that in the following stage—i.e., Stage VIII—of *A. australis*, the number of setae is the same as in the corresponding—i.e., Stage VII—stage of *A. erythraeus*.

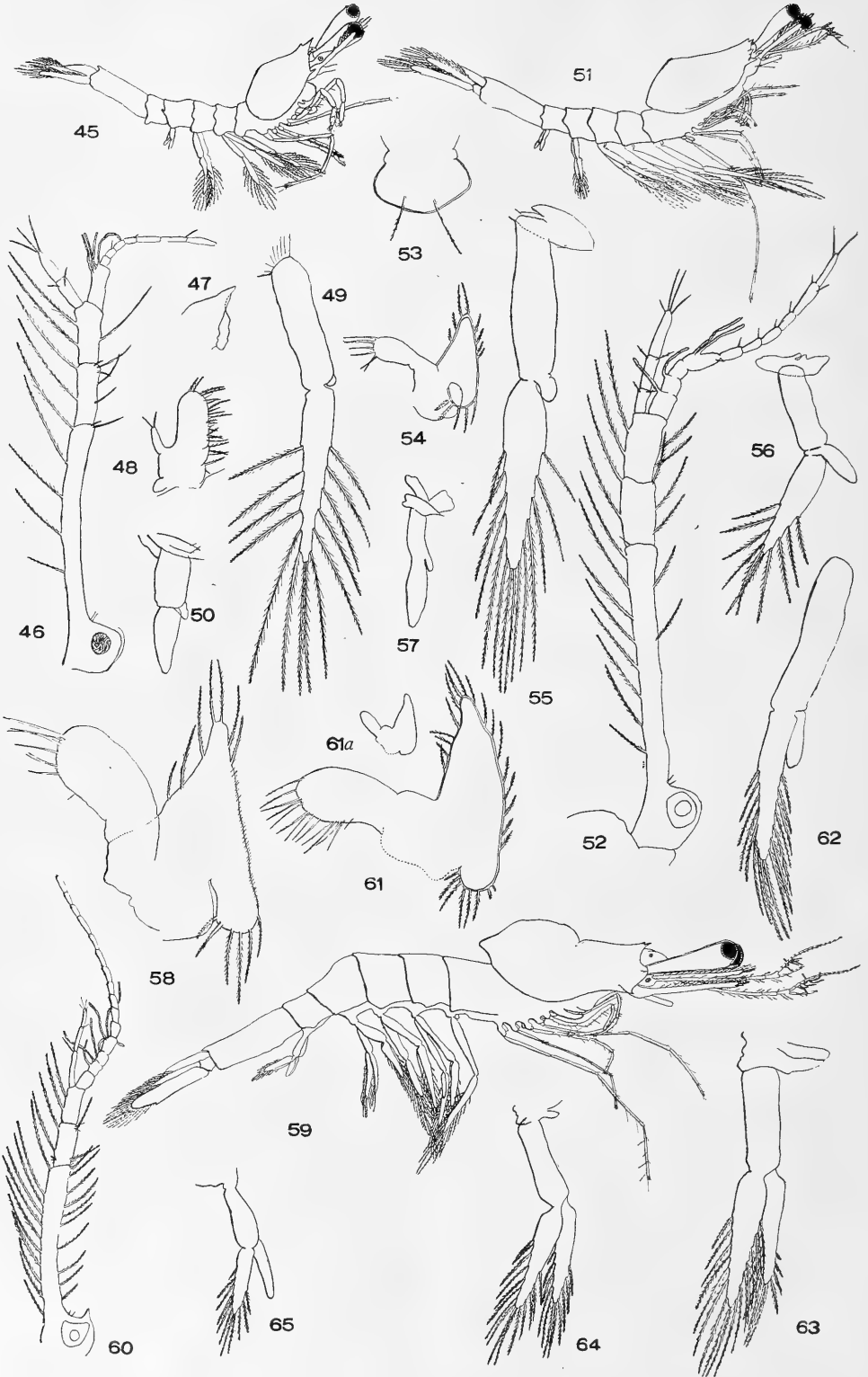
STAGE VIII.

Length from base of rostrum to end of sixth abdominal segment is 2.5 mm.

In some specimens examined there was still no trace of the spine referred to by Menon as occurring in Stage VII of *A. erythraeus* at the outer distal margin of the statocyst swelling of the antennule. However, in some of the specimens examined, there was a definite "squaring" of the swelling at this point. (It will be noted below in Stage IX that the small spine occurs in this position.)

The second maxilla (Text-fig. 58) now resembles the appendage described by Menon for Stage VII of *A. erythraeus* in possessing a small seta about the middle of the proximal border of the endite. The endite, however, bears only six to seven setae, whereas Menon describes eight in his Stage VII and there is still no sign of the rudimentary palp on the endite. The number of setae on the endite increases in the following stages (Stage X, second maxilla, Text-figs. 61–61a), there being usually the same number as in *A. erythraeus*. It should be noted that there is no sign in any of the stages described of a palp on this endite in *A. australis*.

The only change in the pleopods is an increase in the number of setae—the exopodites of first two pairs bearing 16; of the third, 14; of the fourth, 12. Thus they differ from the corresponding appendages in *A. erythraeus* only in the presence of an endopodite on the fifth pair.



It would seem that although this stage agrees closely with Stage VII of *A. erythraeus*, it represents an "early" Stage VII.

STAGE IX.

Length from base of rostrum to end of sixth abdominal segment is 3.3 mm.

This stage corresponds almost exactly with Stage VIII in *A. erythraeus*.

There is now the definite beginnings of a spine on the swelling at the base of the antennule. This is quite an important character as it is one of the main points of distinction between Mastigopus IV and V.

The first pair of pleopods is now the only uniramous pair, whilst all the exopodites are setous.

The acquisition of setae on the exopodites of the fifth pleopods is more important in distinguishing this stage from the previous one than the acquisition of an endopodite on pleopod two as this endopodite sometimes develops later and sometimes earlier.

A rather puzzling fact which must be noted is that the number of setae borne on the pleopods is less than in Mastigopus IV. However, throughout the study of the whole series, it has been noted time without number that it is the presence or absence of setae on the pleopods and not the actual number borne which is the important factor.

It is not until the next stage (Stage X) of *A. australis* that the third (Text-fig. 63) and fourth (Text-fig. 64) endopodites become setous, whilst they become setous in Stage VIII of *A. erythraeus*. In this respect, this stage (Stage IX) of *A. australis* might be considered as intermediate between stages VII and VIII of *A. erythraeus*, whilst the next stage (Stage X) of *A. australis* might be considered as corresponding with Stage VIII of *A. erythraeus*. However, the number of setae borne on the endite of the second maxilla is almost the same in this stage (Stage IX) of *A. australis* as in Stage VIII of *A. erythraeus*, whilst the number in Stage X of *A. australis* is greater.

STAGE X. (Text-fig. 59.)

Length from base of rostrum to end of sixth abdominal segment is 3.6 mm.

Although this stage is later than any stage figured by Menon, it is not until now that the spine on the antennular swelling (Text-fig. 60) becomes really well developed.

No further stages were drawn or examined fully, but certain features in the gradual assumption of the adult form were selected for study.

In the next stage observed, 3.7 mm. in length, the carapace bears hepatic spines as well as the other spines referred to above; whilst there are two rostral teeth instead of the one present in Stage X. Endopodites of the fifth pleopods are now setous whilst the two remaining spines on the telson have shortened, giving the formerly concave posterior border a flatter appearance (Text-fig. 66).

By the time the 4.7 mm. stage is reached the endopodites of the second pleopods have become setous, whilst the telson spines have shortened further and the posterior border is now slightly convex (Text-fig. 67).

By this time the animal has reached the young adult stage and any further changes lie only in the degree of development of structures which already resemble those of the adult fairly well.

DEVELOPMENT OF THE TELSON.

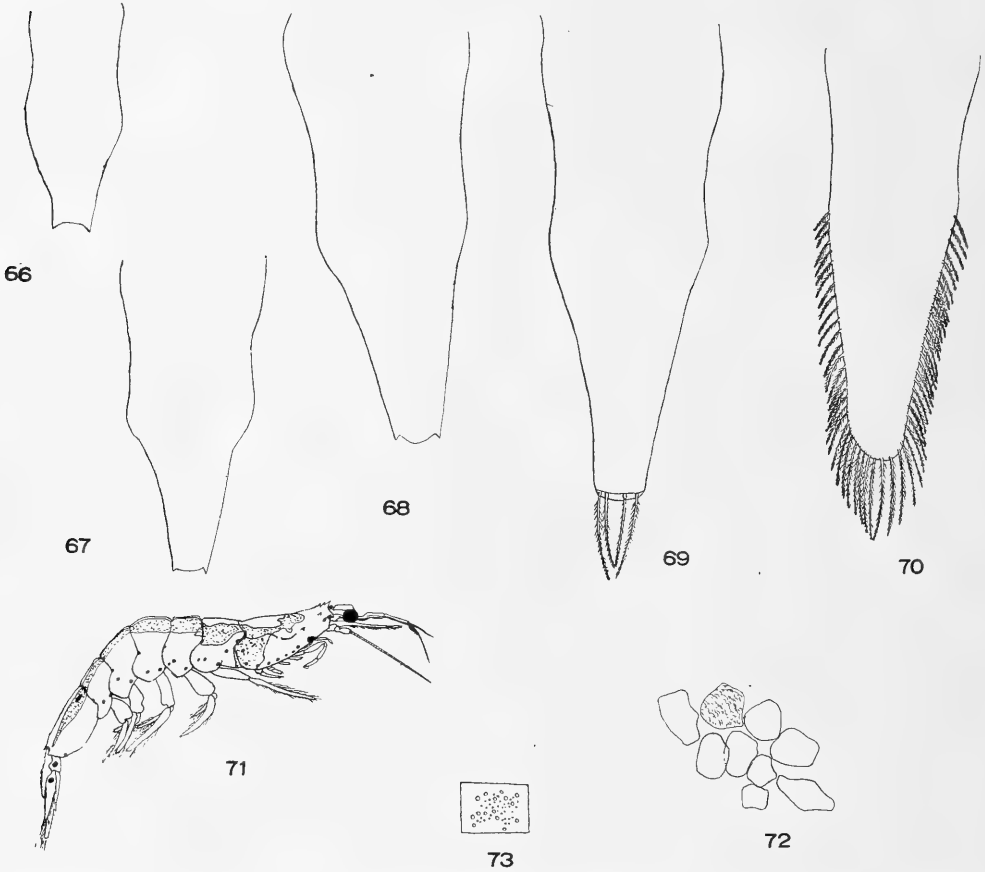
The trend of development of the telson through the stages so far mentioned has been a gradual modification of the Protozoa plan through the loss of spines, shortening of spines, and flattening out of the concave posterior border until finally in the 4.7 mm.

Text-figs. 45 to 50. Stage VI. Text-figs. 51 to 57. Stage VII. Text-fig. 58. Stage VIII.

Text-figs. 59 to 65. Stage X.

45. Stage VI \times 19. 46. Antennule \times 84. 47. Mandible \times 84. 48. First Maxillipede \times 84. 49. Third Pleopod \times 84. 50. Fourth Pleopod \times 84. 51. Stage VII \times 19. 52. Antennule \times 84. 53. Labrum \times 84. 54. Second Maxilla \times 84. 55. Third Pleopod \times 84. 56. Fourth pleopod \times 84. 57. Fifth Pleopod \times 84. 58. Second Maxilla \times 112 approx. 59. Stage X \times 19. 60. Antennule \times 42. 61. Second Maxilla \times 126. 61a. Second Maxilla \times 42. 62. Second Pleopod \times 42. 63. Third Pleopod \times 42. 64. Fourth Pleopod \times 42. 65. Fifth Pleopod \times 42.

stage (Text-fig. 67) it is convex, thus approximating to the adult telson which has a pointed posterior border.



Text-figs. 66 to 70. Telsons.

66. Telson 3.7 mm. Stage $\times 66$ approx. 67. Telson 4.7 mm. Stage $\times 70$ approx. 68. Telson 5.5 mm. Stage $\times 86$ approx. 69. Telson 6.0 mm. Stage $\times 83$ approx. 70. Telson 12.6 mm. Stage $\times 35$ approx.

71. Adult female of *A. australis* showing gonads and red pigment spots $\times 2.5$ approx. 72. Several eggs from gonads $\times 100$. 73. Portion of one egg observed under higher magnification $\times 430$.

By the time the 5.5 mm. stage is reached this convexity is more pronounced (Text-fig. 68), and at the assumption of the 6.0 mm. stage the last traces of the spines have disappeared and the convex posterior border now bears four long setae (Text-fig. 69).

The telson of the 12.6 mm. stage has almost assumed the adult condition. It bears a large number of setae down each lateral margin and on the now pointed posterior border (Text-fig. 70).

DEVELOPMENT OF ANTENNULE.

The basal part of the antennule presents another example of gradual modification in form.

Up to the 4.7 mm. stage the basal segment is rounded in cross-section, but by the time the 5.5 mm. stage (i.e., first young adult) is reached, it has become flattened dorso-ventrally and slightly hollowed out to fit the contour of the eye-stalk. The vertical flap of tissue present on the inner border of the basal segment of the adult antennule is also beginning to develop.

Due to the flattening and consequent broadening in the horizontal plane of this basal segment, the tooth on the distal outer margin of the statocyst swelling now lies closer to the outer border of the basal segment distal to the origin of the tooth. This process of flattening continues until, finally, in the adult, the tip of the tooth and the outer border of the basal segment actually touch enclosing a tiny space (Figs. 2-2a, Colefax, 1940).

DEVELOPMENT OF SECONDARY SEXUAL CHARACTERS IN THE YOUNG ADULT.

The development of the secondary sexual characters presumably does not take place until the animal is almost fully grown, because, in all the young adults observed, there was no sign of the sexual dimorphism which occurs in the antennule of the adult; nor was there any sign of the development of the petasma and modified endopodites of the second pair of pleopods in the male or of the female genital area on the third thoracic sternite.

One or two adult females were taken showing the presence of fully developed gonads. The dense orange-red mass of gonad tissue can be quite easily seen stretching along the dorsal surface, close under the carapace, from the level of the first maxillipede almost to the end of the sixth abdominal segment (Text-fig. 71). A rather large band, running round the body between the last thoracic legs and the first pair of pleopods, can also be distinguished.

TABLE I.
Differences between A. australis and A. erythraeus at Corresponding Stages.

Stage.	<i>A. australis.</i>	Stage.	<i>A. erythraeus.</i>
I	<p><i>Length</i>: 0.35 mm.* <i>Carapace</i>: Longer than broad. <i>Labrum</i>: Short spine. <i>Third Maxillipede</i>: Non-setous (till Stage II). <i>Thoracic Segments</i>: Three behind third maxillipede.</p>	I	<p><i>Length</i>: 0.58-0.59 mm. <i>Carapace</i>: Broader than long. <i>Labrum</i>: Long spine. <i>Third Maxillipede</i>: Setous. <i>Thoracic Segments</i>: Four behind third maxillipede.</p>
II	<p><i>Length</i>: 0.7 mm. <i>Carapace</i>: Anterior spines no longer forked. <i>Mandible</i>: Serrations on seventh tooth.</p>	II	<p><i>Length</i>: 0.92 mm. <i>Carapace</i>: Anterior spines forked (until Stage III). <i>Mandible</i>: Serrations on fourth tooth.</p>
III	<p><i>Length</i>: 1.0 mm. approx. <i>Mandible</i>: No serrations on seventh and eighth teeth. <i>First Maxilla</i>: Five teeth on proximal lobe, six on distal (fewer teeth than in <i>A. erythraeus</i> in all follow-stages). <i>Pleopods</i>: No sign of buds (until Stage IV).</p>	III	<p><i>Length</i>: 1.4 mm. <i>Mandible</i>: Serrations on seventh and eighth teeth. <i>First Maxilla</i>: Six teeth on proximal lobe, seven on distal. <i>Pleopods</i>: Buds.</p>
IV	<p><i>Length</i>: 1.8 mm. approx. <i>Carapace</i>: Supra-orbital spines. <i>Antennule</i>: No peduncular swelling (until Stage V); outer flagellum not segmented (until Stage V); always fewer segments than in <i>A. erythraeus</i>. <i>N.B.</i>—Mouth parts lag behind those of <i>A. erythraeus</i> in development. <i>Labrum</i>: Spine still present (until end of Stage V). <i>First Maxilla</i>: Exopodite remains (until Stage V). <i>Second Maxilla</i>: Protopodite prominences still present; endopodite still segmented and setous. <i>N.B.</i>—"Scaphognathite" always has fewer setae than in <i>A. erythraeus</i>. <i>First Maxillipede</i>: Endopodite present (until Stage V). <i>Telson</i>: Four pairs spines.</p>	IV	<p><i>Length</i>: 2.3 mm. <i>Carapace</i>: No supra-orbital spines (until Stage V). <i>Antennule</i>: Peduncular swelling; outer flagellum faintly segmented. <i>Labrum</i>: Labral spine gone. <i>First Maxilla</i>: Exopodite gone. <i>Second Maxilla</i>: All protopodite prominences except one gone; endopodite gone. <i>First Maxillipede</i>: Endopodite gone. <i>Telson</i>: Six pairs spines (until Stage V.)</p>

TABLE 1.—Continued.
Differences between *A. australis* and *A. erythraeus* at Corresponding Stages.—Continued.

Stage.	<i>A. australis</i> .	Stage.	<i>A. erythraeus</i> .
V	<p>Length: 1.9 mm. approx. Labrum: Spine still present. First Maxillipede: Epipodite present in some (definitely present in Stage VI). Second Maxillipede: Exopodite gone. Third Maxillipede: Exopodite gone. Thoracic legs: Uniramous. Pleopods: Exopodite of second pleopod bears 14 setae. Telson: One pair spines.</p>	V	<p>Length: ? Labrum: No spine. First Maxillipede: Epipodite definitely present. Second Maxillipede: Exopodite still present (until Stage VI). Third Maxillipede: Exopodite still present (until Stage VI). Thoracic legs: Still biramous (until Stage VI). Pleopods: Exopodite of second pleopod bears 12 setae. Telson: Two pairs spines.</p>
VI	<p>Length: 2.2 mm. approx. Antennule: Inner flagellum two-segmented. Telson: One pair spines.</p>	VI	<p>Length: 3.0 mm. Antennule: Inner flagellum not segmented (until Stage VII—then is three-segmented). Telson: Two pairs spines.</p>
VII	<p>Length: 2.5 mm. approx. N.B.—Actually intermediate between Stages VI and VII of <i>A. erythraeus</i>. Antennule: No spine on peduncular swelling. Labrum: Pair of fine ventral spines. Second Maxilla: No seta on middle of proximal border (until Stage VIII); endite bears 6-7 setae; no rudimentary palp on endite. Pleopods: Fifth pair biramous; fewer setae on exopodites than in <i>A. erythraeus</i>. Telson: One pair spines.</p>	VII	<p>Length: 3.5 mm. Antennule: Spine on peduncular swelling. Labrum: No such spines described. Second Maxilla: Seta on middle of proximal border; endite bears eight setae; rudimentary palp on endite. Pleopods: Fifth pair uniramous. Telson: Two pairs spines.</p>
VIII	<p>Length: 2.8 mm. approx. N.B.—This corresponds with Stage VII of <i>A. erythraeus</i> and so will be compared with that Stage, and not with Stage VIII of <i>A. erythraeus</i>. Antennule: "Squaring" of peduncular swelling. Second Maxilla: Endite bears 6-7 setae; no rudimentary palp on endite. Pleopods: Fifth pair biramous.</p>	VIII	<p>Length: 3.5 mm. Antennule: Peduncular spine definitely present. Second Maxilla: Endite bears 8 setae; rudimentary palp on endite. Pleopods: Fifth pair uniramous.</p>
IX	<p>Length: 3.7 mm. approx. Antennule: Peduncular spine beginning. Pleopods: Endopodites of third and fourth pleopods non-setous (until Stage X).</p>	IX	<p>Length: 4.0 mm. Antennule: Peduncular spine definitely present. Pleopods: Endopodites of third and fourth pleopods setous.</p>

* In this table, for purposes of comparison, the lengths for the different stages of *A. australis* take into account the length of the telson which was excluded in the original measurements. Thus from Stage III onwards, the measurements do not agree with those given in the text. As the measurements of the telson had to be made from the figures and not from the original specimens, the figures given in this table, from Stage III onwards, are only approximate.

The eggs show up very clearly in the gonad tissue as a large number of darker circles. The eggs are held in a gelatinous matrix, and are most irregular in shape, the average size being 0.15 to 0.20 mm. at the widest point (Text-fig. 72). They have a very granular appearance due to the presence of a great number of what appear to be globules, possibly fat globules (Text-fig. 73). This granular substance is almost certainly yolk.

As this seems to be the only reference to the appearance of mature gonads and eggs in any member of the genus *Acetes*, and since only a few females showing gonads were taken, it is felt that the figures must be regarded with a certain amount of reserve.

The gonad tissue seems to be in the same position as in other members of the Penaeidae, but the form of the eggs differs quite markedly from the usual form of Penaeid eggs. They are very irregular in shape, and are completely filled with what appears to be yolk, thus lacking the wide gelatinous sheath which is found surrounding most Penaeid eggs. However, as was noted above, the eggs are all held together in a gelatinous matrix, and so it is quite probable that this matrix represents the gelatinous sheath found in Penaeid eggs.

It appears that *A. australis* breeds throughout practically the whole twelve months of the year, as evidenced by the spasmodic appearance of larval stages in several of the catches made throughout the year. In spite of this fact, however, the only times that mature females with ripe gonads appeared in the catches were in late December, 1946, and January, 1947, although adults without gonads were taken quite frequently throughout the year. In this respect, it is very interesting to note that the fullest series of stages was taken in the February catches of 1946. It might be dangerous, but nevertheless tempting, to suppose that the most active period of breeding is during mid- and late summer, hence the appearance of mature females with ripe gonads in December and January and the large number of larvae of all stages in February, and that during the rest of the year, breeding is very spasmodic, as evidenced by the absence of mature females from the catches and the comparatively small number of larval stages caught.

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CYTOLOGICAL STUDIES IN THE MYRTACEAE.

II. CHROMOSOME NUMBERS IN THE LEPTOSPERMOIDEAE AND MYRTOIDEAE.*

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(Plates i and ii; ninety-one Text-figures.)

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INTRODUCTION.

As the dominant family in the vegetation of Australia, the Myrtaceae also rank first in economic importance, chiefly owing to the hardwood timbers produced by *Eucalyptus* and a few other genera. The whole family is characterized by the occurrence of oil glands in the leaves, and many genera produce essential oils of actual or potential value.

Considerable confusion has existed and still exists in the systematics and taxonomy of many of the larger genera, especially in the dominant tribe Leptospermoideae. Differences of opinion exist on the status of species, and on the occurrence and importance of hybridization both within and between species. In *Eucalyptus*, Maiden (1924), Cambage (cit. Maiden, 1924) and Blakely (1934) have assumed that in many cases named species are of hybrid origin and have often suggested probable parents for particular species. Maiden accepted hybridization as a process in species formation. On the other hand, Mueller and Woolls (cit. Maiden, 1924) and Hall (1914) have minimized the importance of hybridization in the genus, and Baker and Smith (1920) deny its importance and consider it a rare and abnormal occurrence. Lawson (1930), however, has shown that in many genera and species the extent of pollen sterility is suggestive of their origin by hybridization, and Brett (1937) claims that some Tasmanian species of *Eucalyptus* are F₁ hybrids, whilst others are complex species or hybrid segregating swarms. In other genera, species are often extremely variable, but the extent of hybridization within or between species is practically unknown. Cheel (private discussion) accepts the occurrence of interspecific hybridization in *Leptospermum* and *Callistemon*. Cockayne (1923), Cockayne and Allen (1934) and

* For Part i, see these PROCEEDINGS, Vol. LXVII: 335.

Allen (1931, 1937) have shown that in an endemic flora hybridization may be an important factor, and they have described the occurrence of hybrid swarms in the polymorphic New Zealand species *Leptospermum scoparium*.

The value of cytological data in the interpretation of the taxonomy and phylogeny of any group has been discussed by many authorities, and Anderson (1937) has pointed out that this value will depend on the cytological stability of the particular group. In a natural group, evolutionary trends are likely to remain discernible, and, depending on the processes involved, cytological data may be of considerable value in the interpretation of the status of species and of their relationships. Cytological data may be used to show the processes involved in evolution (Babcock, 1942), to support taxonomic systems based on morphology, or to modify them, to establish unsuspected relationships, as between *Yucca* and *Agave* (McKelvey and Sax, 1933, Whitaker, 1934), or to justify the splitting of genera and species into two or more new ones. In many cases the method of origin of species may be indicated.

THE TAXONOMY OF THE MYRTACEAE.

The Myrtaceae is included in the Order Myrtiflorae (Myrtales), which, according to Hutchinson (1926), includes five families, the Rhizophoraceae, Combretaceae, Myrtaceae, Lecithidaceae and Melastomaceae. The Order as thus defined is a more natural one than that of Bentham and Hooker (1862-67) or of Engler and Gilg (1924). According to Sprague (1939) the Myrtales (sensu Bentham and Hooker) constitutes a natural group, and Atchison (1947) considers that the constancy in chromosome numbers throughout the family Myrtaceae supports its designation as a natural group.

The family is itself divided into three tribes, the Chamaelaucoideae, Leptospermoideae, and Myrtoideae. The first two tribes are often combined as a Subfamily Leptospermeae, in which case the third tribe would also constitute a subfamily. The Tribe Leptospermoideae is further subdivided into five subtribes, some of which may have had separate origins.

THE DISTRIBUTION OF GENERA AND SPECIES.

The distribution of the family has been summarized by Andrews (1913) and has been referred to by Atchison (1947). The Myrtoideae is chiefly tropical South American in occurrence, but there is a smaller centre of diversity in South-west Asia, and five or six genera occur in eastern Australia. The tribe is completely absent from Western Australia. On the other hand, the Chamaelaucoideae and the Leptospermoideae, with the exception of the subtribe *Metrosiderae*, are almost confined to Australia, and have their main centres of diversity in southern Western Australia. The subtribe *Metrosiderae* is a Polynesian and Indonesian group which appears to have entered Australia with the Malayan intrusion of mesophytic, rain-forest types, and is absent from Western Australia. In its geographical distribution it is comparable with the Myrtoideae.

PREVIOUS RECORDS OF CHROMOSOME NUMBERS IN THE MYRTACEAE.

Atchison (1947) has compiled all previous records of chromosome numbers for the family, and has added new data for five species of *Psidium* and 26 species of *Eucalyptus*. The records show only few cases of deviations from a haploid number of 11, or of a multiple of this number, and the earlier reports of haploid numbers of 14 in *Eucalyptus* by Harrison (cit. Tischler 1937) and of diploid numbers of 20 in the same genus by Sugiura (1936) would appear to be in error, since subsequent counts of 11 have been obtained for the same species by other workers. The polyploid series on a base 7 reported by Van der Pijl (1934) for *Eugenia jambosa* also requires confirmation. Atchison (l.c.) has reported a diploid number of 24 for two species of *Eucalyptus*, these representing the only examples of deviations from the base number of 11 recently reported for the Leptospermoideae. Atchison has drawn attention to the remarkable uniformity in chromosome number within the family, which is perhaps more pronounced than in any other family of equivalent size.

McAulay and Cruickshank (1937) found indications of secondary associations at the first metaphase in the species examined by them, and Smith-White (1942) suggested

TABLE 1.
Details of the Material.

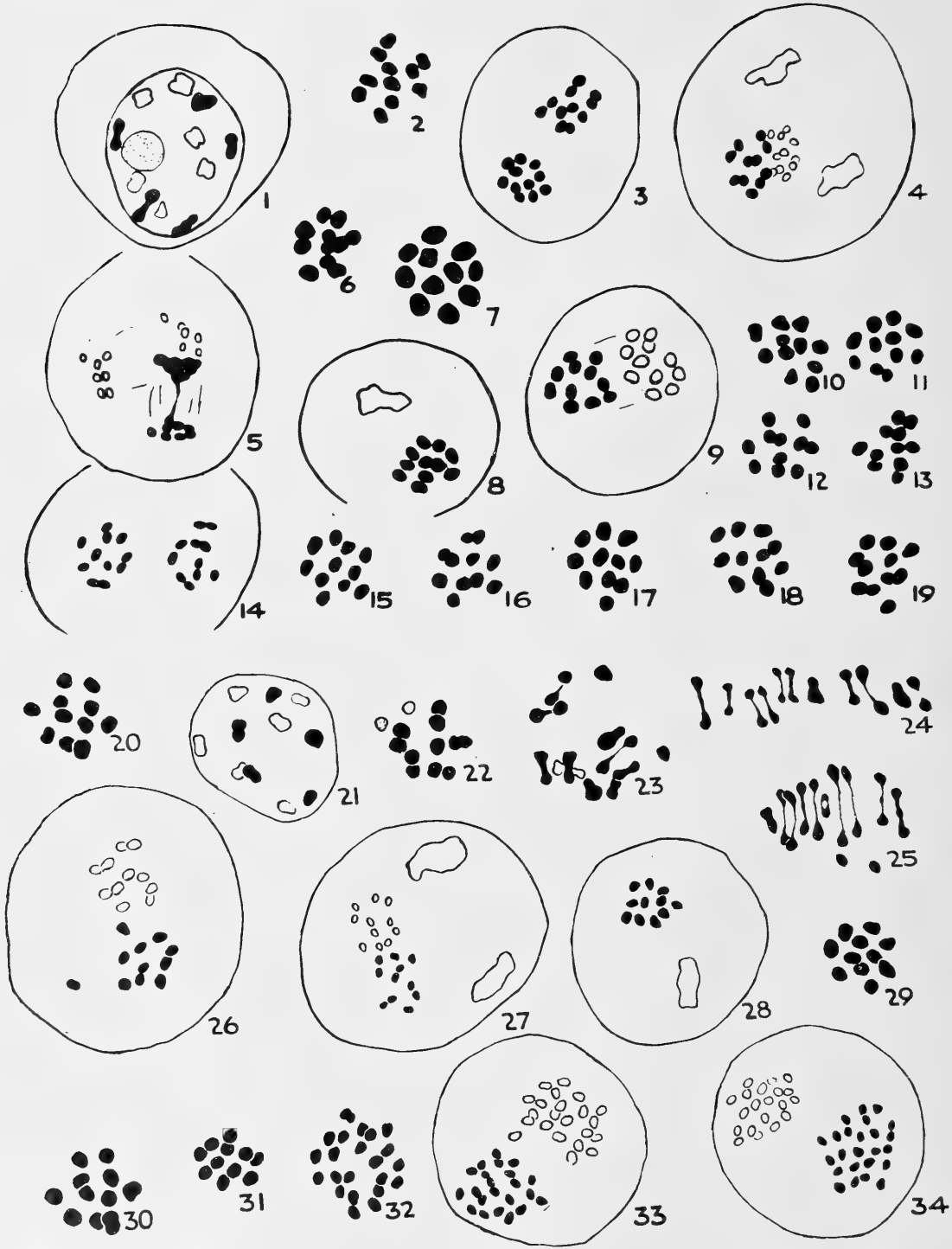
Species.	Occurrence.	Wild or Cultivated.	Localities.	No. of Plants.	Haploid Chr. Number.	Availability of Material.	Pollen Fertility.
TRIBE LEPTOSPERMOIDEAE.							
SUBTRIBE BAECKEAE.							
<i>Baeckea diffusa</i> (Steb.)	N.S.W.	Wild.	Nat. Pk.	3	11	Sept.-Oct.	53.3 ± 5.13%
" <i>crenulata</i> DC.	"	"	Nat. Pk., Curl Curt.	2	11	Sept.-Oct.	
" <i>diomsifolia</i> Rudge	"	"	Kuring-gai.	2	11	Sept.-Oct.	
" <i>hircifolia</i> Rudge	"	"	Gordon, L.C.R.	2	11	Sept.-Nov.	
" <i>densifolia</i> Sm.	"	"	Gordon, L.C.R.	3	11	Nov.-Jan.	90%
SUBTRIBE EULEPOSPERMEAE.							
<i>Aponis flavosa</i> Schau.	W.A.	Cult.	S.B.G.	2	11	Oct.-Nov.	96.3 ± 1.51%
<i>Leptospermum laevigatum</i> F. v. M.	N.S.W.	Wild.	Nat. Pk., Austimmer.	3	11	Aug.-Oct.	99.7 ± 0.16%
" <i>flavescens</i> Sm.	"	"	Gordon.	2	11	Sept.-Oct.	
" <i>flavescens</i> v. <i>leptophylla</i>	"	"	Ashfield.	1	11	Sept.	0%
" <i>citratum</i> Chal. Cheel and Penfold	"	Cult.					
" <i>citratum</i> var. "A"	"	"	Gordon, Nat. Pk.	5	11	Dec.-Jan.	
" <i>leversidgei</i> B. and S.	"	"	Gordon.	3	11	Dec.-Jan.	
" <i>persicaeflorum</i> Reichb.	"	Cult. and wild.	Gordon, Coff's Harb.	3	11	Nov.-Jan.	
" <i>juniperinum</i> Sm.	"	"	Gordon.	2	11	Nov.-Jan.	
" <i>sandersi</i> (Hort.)	N.Z.	"	Kuring-gai, Braidwood.	3	11	Nov.-Dec.	92.0 ± 1.67%
" <i>arachnoideum</i> Sm.	"	Cult.	Gordon.	1	11	Nov.-Dec.	
" <i>lanigerum</i> Sm.	N.S.W.	Wild.	Austimmer, Gordon.	3	11	Oct.-Nov.	
" <i>grandifolium</i> Sm.	"	"	Gordon.	3	11	Nov.-Dec.	53.3 ± 2.60% - 6.80 ± 1.51%
" <i>parvifolium</i> Sm.	"	"	L.C.R.	3	11	Sept.-Nov.	98.3 ± 1.83%
" <i>stellatum</i> Cav.	"	"	L.C.R.	5	22	Aug.-Sept.	63.3 ± 2.13%
" <i>rotundifolius</i>	"	"	Nat. Pk., Gordon.	4	11	Sept.-Nov.	5.5 ± 2.01% - 80.9 ± 1.97%
<i>Kansea corifolia</i> Reichb.	N.S.W.	Cult.	Nat. Pk., Gordon.	2	11	Sept.-Oct.	91.6 ± 2.08%
" <i>capitata</i> Reichb.	"	Wild.	Nat. Pk., Gordon.	3	11	Sept.-Nov.	
" <i>copitata</i> Reichb.	"	"	Gordon.	2	11	Sept.	
" <i>Callistemon phoenicis</i> Lindl.	W.A.	Cult.	S.B.G.	2	11	Sept.-Oct.	93.25 ± 1.01%, 92.5 ± 0.90%
" <i>lanceolatus</i> DC.	E.A.	Wild.	Gordon, L.C.R.	11	11	Sept.-Nov.	Table 3
" <i>pauciflygulus</i> Cheel.	N.S.W.	Cult. and wild.	Gordon, Coff's Harb.	3	11	Sept.-Nov.	94.25 ± 0.53%
" <i>tiliacina</i> Cheel	"	"	Gordon, Coff's Harb.	2	11	Sept.-Nov.	97.75 ± 0.71%, 96.4 ± 0.73%
" <i>hortensis</i> Cheel	?	"	S.B.G.	2	11	Sept.-Oct.	78.1 ± 1.55%
" <i>comboyensis</i> Cheel	N.S.W.	"	Ashfield, S.B.G.	2	11	Sept.-Oct.	
" <i>acuminatus</i> Cheel	"	"	Ashfield.	1	11	Oct.-Nov.	98.0 ± 0.32%, 52.5 ± 3.40%
" <i>rugulosus</i> DC.	S.A.	"	S.B.G., Gordon.	3	11	Aug.-Sept.	7.25 ± 2.05%, 4.88 ± 1.15%
" <i>subulatus</i> Cheel	N.S.W.	"	S.B.G.	2	11	Sept.-Oct.	
" <i>subulatus</i> Cheel	"	"	S.B.G.	2	—	Aug.-Sept.	

L.C.R. = Lane Cove River. S.B.G. = Sydney Botanic Gardens.

TABLE 1.—Continued.
Details of the Material.—Continued.

Species.	Occurrence.	Wild or Cultivated.	Localities.	No. of Plants.	Haploid Chr. Number.	Availability of Material.	Pollen Fertility.
TRIBE LEPTOSPERMOIDEAE.—Cont.							
SUBTRIBE EULEPTOSPERMEAE.—Cont.							
<i>Callistemon rigidus</i> R.Br.	N.S.W.	Cult. and wild.	Gordon, L.C.R.	13	11, 22	Aug.-Oct.	Very low.
" <i>linearis</i> DC.	"	"	Gordon, Fairfield, Yagoona, L.C.R., S.B.G.	30	11, ca. 33/2, 22	Aug.-Oct.	Very variable, 0-30%
" <i>paniculatus</i> DC.	"	"	Yagoona, S.B.G., Gordon, Fairfield.	18	11, ca. 33/2, ca. 33/2	Aug.-Oct.	Usually very low, 5%
" <i>salignus</i> DC.	"	"	Gordon, Coff's Harb.	5	11	Aug.-Sept.	
" <i>speciosus</i> DC.	W.A.	Cult.	Concord West.	1	11	Sept.-Nov.	
" <i>vininialis</i> Sol.	Qld.	"	Gordon.	6	22	June-Sept.	
<i>Melaleuca lateralis</i> Otto.	W.A.	"	Gordon.	4	11	July-Sept.	87.13±2.11%
" <i>elliptica</i> Labill.	"	Wild.	Aunstinmer.	1	11	Aug.-Sept.	69.7±5.95%—99.0±0.27%
" <i>hypericifolia</i> Sm.	N.S.W.	"	National Park.	3	11	Sept.-Nov.	
" <i>thymifolia</i> Sm.	"	"	Concord.	2	11	Sept.	
" <i>ericifolia</i> Sm.	"	Cult.	National Park.	1	11	Aug.-Sept.	
" <i>linariifolia</i> Sm.	"	Wild.	National Park.	1	11	Aug.-Sept.	
" <i>alternifolia</i> Cheel	"	Cult.	Nat. Pk., Gordon.	2	11	Aug.-Sept.	
" <i>armillaris</i> Sm.	"	"	Nat. Pk., S.B.G.	2	11	Aug.-Sept.	
" <i>Smithii</i> Baker	"	"	Nat. Pk.	1	11	Aug.-Sept.	High over 90%
" <i>stypheoides</i> Sm.	"	"	S.B.G.	1	11	Aug.-Sept.	
" <i>nodosa</i> Sm.	"	"	Nat. Pk., S.B.G.	2	11	Aug.-Sept.	
SUBTRIBE BEAUFORTEAE.							
<i>Calothamnus villosus</i> R.Br.	W.A.	"	S.B.G., Gordon.	3	11	Sept.-Oct.	Uniformly high, 90%
SUBTRIBE EUCAALYPTEAE.							
<i>Eucalyptus citriodora</i> Hooker	Qld.	Wild.	Gordon, Grafton.	2	11	Sept.	
" <i>paniculata</i> Sm.	N.S.W.	Cult.	Gordon.	3	11	Sept.	High, over 90%
" <i>dioses</i> Schau.	"	"	Gordon.	4	11	Aug.-Sept.	0%—69.0±1.34%
" <i>Behriana</i> F. v. M.	W.A.	"	Gordon.	1	11	June-July.	
" <i>tetraptera</i> Turcz.	N.Qld.	"	S.B.G.	1	11	Feb.	High, 90%.
" <i>stangeriana</i> F. v. M.	"	"	Gordon.	2	11	Feb.-March.	
SUBTRIBE METROSIDEREAE.							
<i>Tristania laurina</i> R.Br.	N.S.W.	Wild.	Nat. Pk.	2	11	Sept.	
<i>Syncarpia laurifolia</i> Ten.	"	"	Gordon.	2	11	Sept.	High, over 90%.
<i>Boehavia myrtifolia</i> Hooker and Harvey	"	"	Nat. Pk.	2	11	Sept.	
TRIBE MYRTOIDEAE.							
<i>Eugenia smithii</i> Pol.	"	Wild and cult.	Nat. Pk., Gordon.	3	22	Nov.-Dec.	
" <i>myrtifolia</i> Sims.	"	"	Gordon, Nat. Pk.	3	22	Nov.-Dec.	92.9±0.77%
" <i>leuimanni</i> F.v.M.	"	Cult.	S.B.G.	1	22	Nov.-Dec.	
<i>Psidium cattleianum</i>	Brazil.	"	S.B.G.	1	ca. 44	Oct.-Dec.	

L.C.R. = Lane Cove River. S.B.G. = Sydney Botanic Gardens.



Text-figs. 1-34.

Figs. 1-5. *Baeckea diffusa*. 1. Diakinesis. 2. 1-M. 3. 2-M, showing some secondary association. 4. 2-A, showing secondary association in five pairs. 5. 2-A, with a second division bridge. Fig. 6. *B. linifolia*, 1-M. Figs. 7 and 8. *B. densifolia*. 7. 1-M. 8. 2-M. Note the relatively large size of the chromosomes. Fig. 9. *Agonis flexuosa*, 1-A. Fig. 10. *Leptospermum*

that the haploid complement of 11 might prove to be derived from a basic number of seven. Atchison (1947) doubts the validity of this hypothesis on the grounds of the constancy of numbers and the supposed antiquity of the family, which, according to Andrews (1913), dates at least from the Lower Cretaceous.

MATERIALS AND METHODS.

The species reported in the present paper are listed in Table 1, which also indicates the source, number of plants studied and seasonal availability of material for each species. In the table the genera and species are arranged according to the system of Bentham in the *Flora Australiensis* (1866).

Most of the species studied are native to the sandstone flora in the vicinity of Sydney, and of these abundant material has been available. Species native to other parts of the continent have been examined from cultivated trees and shrubs, and in some cases this horticultural material may not be representative of the species in nature.

The work was concerned chiefly with meiotic stages during microsporogenesis, using temporary acetocarmine crushes prepared by the technique previously described (Smith-White, 1942). An alternative method of maceration on the slide with acetocarmine containing 1% of HCl, similar to the method described for aceto-orcein by Darlington and La Cour (1942) was found useful for materials stored in 70% alcohol. The description of prophase development in *Eucalyptus paniculata* is from sectioned material fixed in Randolph's CRAF modification of Navashin's fluid (1935) and stained in iron haematoxylin. Examination of pollen for viability was made in a dextrin-sorbitol fluid similar to that described by Zirkle (1940), in which the carmine was replaced by sufficient of a mixture of 3 parts 1% acid fuchsin and 1 part 1% light green. Such slides do not require sealing, and have been kept in excellent condition for over three years. A similar gelatin-sorbitol mountant gave unsatisfactory staining.

Drawings were made with a camera lucida at a magnification of ca. 3900, and have been reduced in reproduction to ca. 2600. Photographs are at a magnification of 2000 times except in the case of pollen photographs, which are at a magnification of ca. 240.

CYTOLOGY OF THE GENERA AND SPECIES.

TRIBE LEPTOSPERMOIDEAE.

Subtribe Baeckeeae.

This subtribe contains six genera, of which four are restricted to Western Australia. The genus *Scholtzia* connects it with the Chamaelaucoideae.

Baeckea Linn. A genus of 45-50 species, divided into six sections. Three of these are restricted to Western Australia, and the five species recorded here include representatives of the other three sections. All five species have a haploid chromosome number of 11 (Text-figs. 1-8) and show regular chromosome behaviour.

In *B. diffusa*, first and second metaphase plates show typically considerable secondary association (Text-figs. 2, 3, 4). The chromosomes are often so crowded that a clear analysis of this association is difficult, but it is rarely less than three pairs. Rarely chromosome bridges are seen at 1-A or 2-A (Text-fig. 5), indicating the existence

laevigatum. 1-M. Figs. 11-14. *Leptospermum flavescens*. 11-13. 1-M, showing degrees of secondary association. 14. 2-M. Fig. 15. *L. flavescens* var. *leptophylla*. 1-M, showing normal bivalent formation. Fig. 16. *L. liversidgei*. 1-M. Fig. 17. *L. sandersi*. 1-M. Fig. 18. *L. juniperinum*. 1-M. Fig. 19. *L. arachnoideum*. 1-M. Fig. 20. *Leptospermum lanigerum*. 1-M. Figs. 21-27. *L. grandifolium*. 21. Late diakinesis. 22. 1-M, showing two univalents. 23. Early 1-A, in a flattened cell. The two apparent univalents may be due to precocious separation of a bivalent. 24 and 25. Side views of early 1-A. In 24 the univalents appear to be due to precocious separation, but in 25 they are true univalents judging by their position. Note that most bivalents are associated by single terminal chiasma, but occasionally the two chromosomes of a bivalent may be associated by two terminal chiasma. 26. 2-M. 27. 2-A, showing marked secondary association. Figs. 28 and 29. *L. stellatum*. 28. 2-M. 29. 1-M. 30. *L. rotundifolia*. Fig. 31. *L. citratum*, var. A. 1-M. Figs. 32-34. *L. parvifolium*. 32. 1-M. 33 and 34. 2-M. 34 shows unequal (24/20) 2-M plates. Both figures show the occurrence of secondary associations of more than two chromosomes. All \times ca. 2,600.

of heterozygosity for a small inversion. In *B. densifolia*, the chromosomes at 1-M appear somewhat larger than in the other species, and secondary association is less evident, although a critical examination of this feature was not made.

Subtribe Euleptospermeae.

This subtribe includes seven genera, three being confined to Western Australia.

Agonis DC. This genus includes about 10 species, of which one is cultivated to some extent around Sydney. *A. flexuosa*, the only species examined, has a haploid chromosome number of 11 (Text-fig. 9), and shows quite regular chromosome behaviour, but both trees examined showed a pollen sterility amounting to about 50%, the aborted pollen being of small size, empty of protoplasm, but of regular shape (Plate ii, fig. 17). In 38 pollen mother cells at 1-M, and in 76 at 1-A, no irregularities of chromosome behaviour were seen, and 106 cells at interphase were all normal. Regular tetrad formation was uniformly found in a count of 344 cells at this stage. It would appear that the high degree of pollen sterility (cf. Table 1) cannot be explained by any gross structural differences in the chromosomes.

Leptospermum Forst. A genus of about 30 species, widespread throughout the continent, and extending to New Zealand. The genus is divided into three sections. Of the 14 species examined, all except *L. parvifolium* have a haploid chromosome number of 11 (Text-figs. 10-30), with regular chromosome behaviour, and with pronounced but variable secondary association (Table 5).

Pollen fertility was found to be high in most species (Table 1), of the order of 90-99% (Plate ii, figs. 18, 19), but in a cultivated plant of *L. flavescens* var. *leptophylla*, the pollen was entirely aborted, and the plant was practically seed sterile. It carries thousands of flowers each year, but sets only one or two capsules. This sterility did not appear to be caused by any cytological unbalance, since the meiotic divisions all appeared normal, with regular chromosome pairing (Text-fig. 15). The cause of the seed and pollen sterility may prove merely environmental, since the variety is restricted to the North Coast of New South Wales, some 350 miles north of Sydney (Cheel, cf. Penfold, 1922), but it is more probably genetical in nature.

Other species show a variable degree of pollen fertility, ranging, in individual plants, from 50-98%, and this variation is pronounced in *L. stellatum*. Four plants of this species were found to have a pollen fertility of $80.9 \pm 1.97\%$, $39.5 \pm 1.08\%$, $32.9 \pm 2.32\%$ and $5.5 \pm 2.01\%$ respectively. The plant showing the greatest pollen sterility appeared to be in no way different from the others, and observed irregularities of behaviour during meiosis were quite insufficient to account for the condition. The sterile pollen was of small size, empty of protoplasm, and of irregular shape (Plate ii, fig. 21).

L. parvifolium is a small, slender, small-leaved shrub, considered by Mueller (cf. Bentham 1866) to be only a variety of *L. lanigerum*. It has, however, a haploid number of 22 (Plate i, fig. 20), and shows a fairly regular meiosis, regular bivalent formation, and a fairly high pollen fertility. The pollen, however, is of relatively large size compared with that of related species (Table 2 and Plate ii, fig. 4), and this is undoubtedly due to its tetraploid constitution.

TABLE 2.
Pollen Size in Leptospermum and Callistemon.

Species.	Haploid Chromosome Number.	Mean Diameter. (Microns.)	Difference. (Microns.)	Volume Ratio (D ³).
<i>Leptospermum lanigerum</i> ..	11	15.5 ± 0.28		
" <i>parvifolium</i> ..	22	21.8 ± 0.35	6.3 ± 0.45	1:2.8
<i>Callistemon lanceolatus</i> ..	11	15.9 ± 0.14		
" <i>viminalis</i>	22	17.7 ± 0.20	1.8 ± 0.24	1:1.4

Secondary association is pronounced, both at 1-M and 2-M (Text-figs. 32, 33), and occasionally irregularities at 1-M or 1-A may result in unequal 2-M plates, a distribution

of 20/24 being found in several cases (Text-fig. 34). These irregularities are not sufficient to cause serious pollen infertility, and the species is essentially allotetraploid in behaviour.

Kunzia Reichb. A genus of about 15 species, divided into two sections. Both species included in the present paper belong to the section *Salisia*, but Cheel (1943) has recently removed *K. corifolia* to *Leptospermum*. Both species have a haploid number of 11 (Text-fig. 35) with regular behaviour, and pollen is of high fertility, exceeding 90% in the plants examined.

Callistemon R.Br. As revised by Cheel (cf. Maiden, 1911), this ornamental genus comprises at least 20 species, and possibly 30 species could be established. It is widespread over Australia, and is closely allied to the larger genus *Melaleuca*. Many of the taxonomic species are of doubtful rank, and Bentham (1866) remarked that they might all be considered as merely varieties of a single species. The genus has been divided by Cheel into two sections, *Eucallistemon* and *Tubuloso-Callistemon*, the latter including two species with the filaments of the stamens united in a short ring.

Cytological conditions and pollen fertility are not uniform in the genus, and it is desirable to treat the species individually in the present paper.

Section Eucallistemon Cheel.

C. phoeniceus, from Western Australia, is closely allied to *C. lanceolatus*. The two plants examined have a haploid number of 11 (Text-fig. 36), have regular meiotic behaviour and pollen fertility exceeding 90% (Table 1).

C. lanceolatus. A widespread eastern species, for which the chromosome number has already been reported (Smith-White, 1942). Darlington and Janaki Ammal (1944) report a haploid number of 11 also for a species *C. citrinus*, a name which ranks as a synonym for this species. The count reported by the present author in 1942 was derived from several cultivated plants, but a similar count has been obtained from wild material in several populations around Sydney (Text-figs. 37-38). In all wild material examined, chromosome behaviour was normal, and pollen fertility was usually found to be high (Table 3 and Plate ii, fig. 22), whereas in cultivated plants considerable chromosome irregularities were found, and pollen fertility was variable and sometimes very low (Plate ii, fig. 23). The cytological conditions found in the cultivated forms will be dealt with in a subsequent paper. The data on pollen fertility in wild plants given in Table 3 indicate that Lawson's data (1930) for the same species is unreliable, and his count was probably made on material from a cultivated tree, or from several cultivated trees. The species has been cultivated in Sydney for many years and the cultivated form is according to Cheel (private communication) of hybrid origin. At any rate, the opportunity for hybridization in the cultivated strains has been considerable, and such material cannot be accepted as typical of the wild species.

TABLE 3.
Pollen Fertility in Callistemon lanceolatus.

Plant No.	1	2	3	4	5	6	7	8	9	10	M
Mean pollen fertility*	96.4	98.4	98.1	98.1	52.2	95.9	99.6	98.5	94.7	96.9	92.9

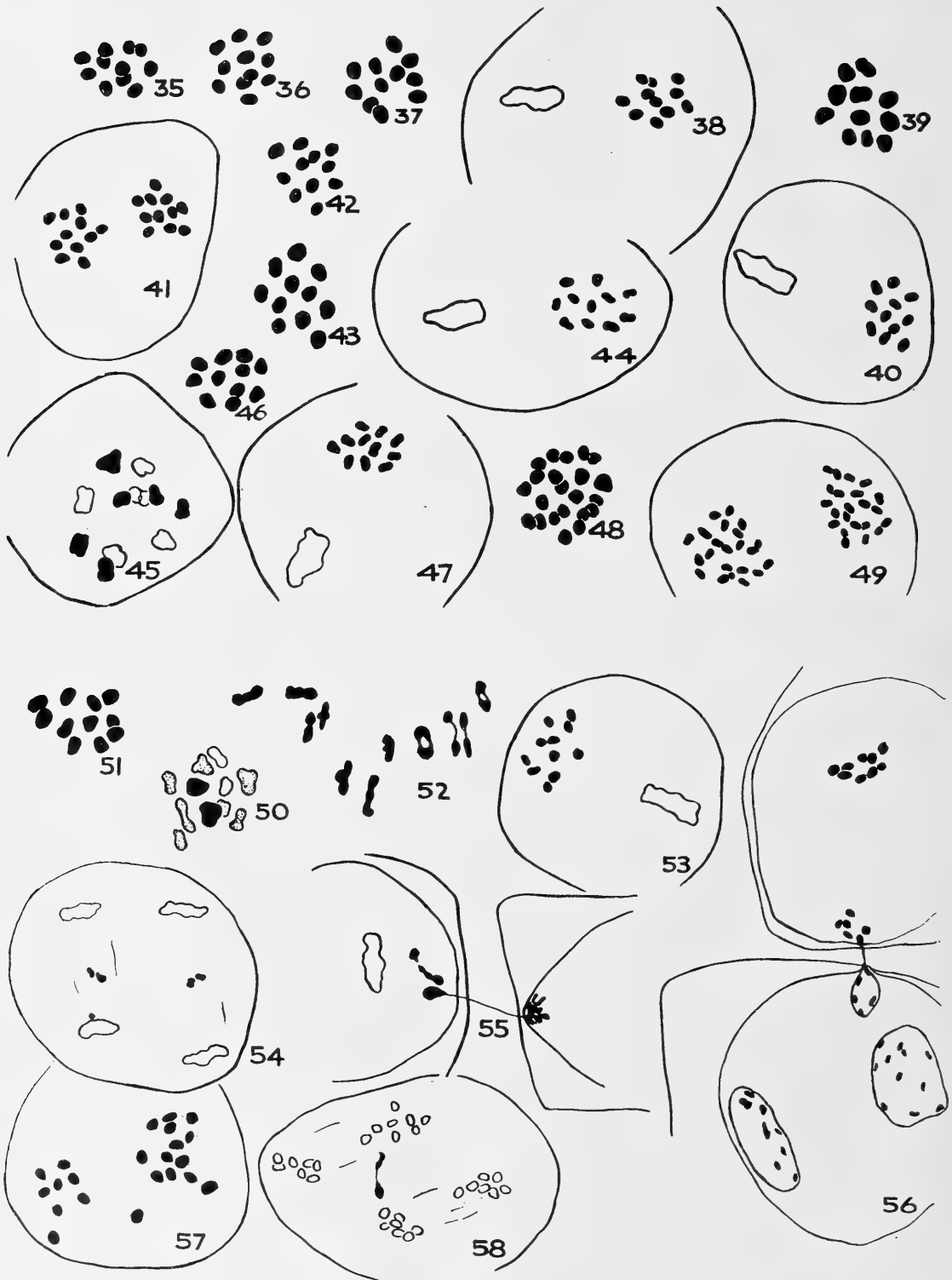
* Means of four determinations from each of two flowers.

Analysis of Variance.

	S.S.	D.F.	M.S.	F.	S.E.	Significant Difference.
Between plants . .	14,829.8625	9	1647.7625	103.06†	1.414	4.46
Between slides*	159.8750	10	15.9875			
Within slides . .	726.2500	60	12.1042			
Total . .	15,715.9875	79				

* Used as error control.

† Greatly exceeds 1% point



Text-figs. 35-58.

C. pachyphyllus. The three plants examined were all raised from seed collected from wild plants by the author. According to Cheel the material examined belongs to the variety *angustifolium* of his species. In the Coff's Harbour locality, from which the seed was obtained, the species shows a wide variation in flower colour, suggestive of Mendelian segregation, but is otherwise quite uniform. A haploid chromosome number of 11 was found in all three plants (Text-figs. 39, 40), and all had regular meiosis, and pollen fertility of about 95% (Table 1).

C. lilacina. A species of the *C. lanceolatus* group, native to the Gosford district. The two plants in the Sydney Botanic Gardens were grown from seed collected by Cheel. Both plants were found to have a haploid number of 11 (Text-fig. 41), regular meiosis, and pollen of high fertility (Table 1).

C. comboynensis. A species from the North Coast of New South Wales which is very closely related to *C. lanceolatus*, from which it differs in characters of perhaps small taxonomic importance, as, for example, in the possession of a fragrant essential oil in its leaves. The only material studied has been a plant grown by Mr. E. Cheel at Ashfield. This plant is notable in being practically seed sterile. Although it has flowered regularly for several years, it has set only two capsules from many thousands of flowers. Very limited material of the plant has been available. The haploid chromosome number for the plant is 11, but it has not yet been determined whether its infertility is due to cytological causes and its pollen has not been examined. Its infertility suggests that it is hybrid in nature.

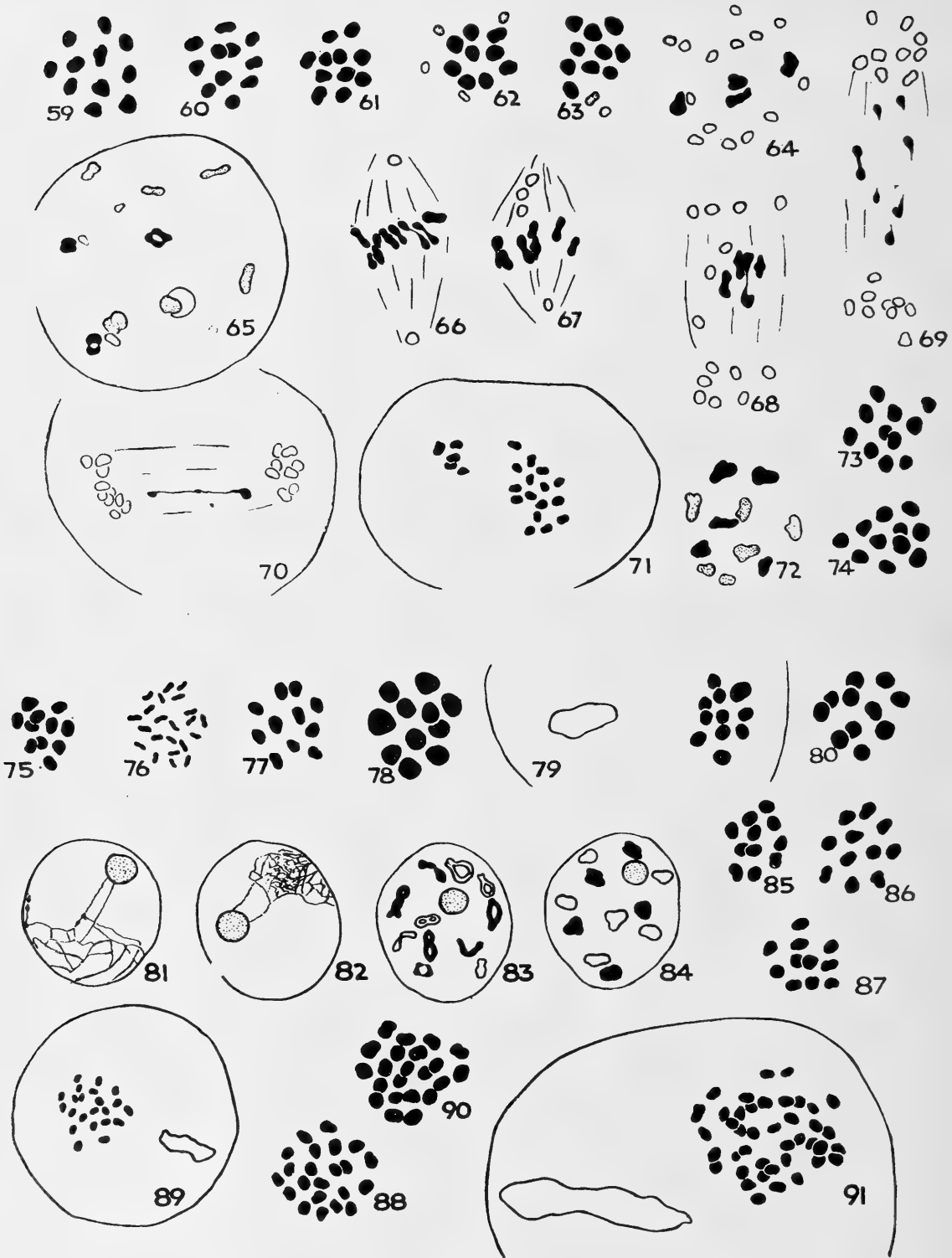
C. hortensis. A species named from several plants raised by Cheel from seed received from Berlin. According to Cheel, it shows a wide segregation in its progeny and is of hybrid nature. Two plants were examined, one grown by Mr. E. Cheel at Ashfield and one at the Sydney Botanic Gardens. In both a haploid chromosome number of 11 was found (Text-fig. 42). Mr. Cheel's plant possessed only fair pollen fertility, $78.1 \pm 1.55\%$.

C. acuminatus. Another species of the *C. lanceolatus* complex, distinguished by its broader, acuminate, thinner-textured leaves. It is a species with a restricted natural range, and material for study was obtained from two plants grown at the Sydney Botanic Gardens from wild seed and from one plant raised by the author from one of these.

The two Botanic Gardens plants both had a haploid chromosome number of 11 (Text-figs. 43, 44; Plate i, figs. 2, 3), regular meiosis and pollen fertility of $98.0 \pm 0.42\%$ and $98.0 \pm 0.50\%$ respectively. The Gordon plant, a seedling from the Sydney Botanic Gardens No. 1 (open pollinated), however, showed pollen fertility of only $52.5 \pm 3.40\%$. Unfortunately the seedling failed to survive before any cytological observations could be made on it. Since opportunity for cross pollination would be considerable in the Gardens, it is possible that the plant was a hybrid.

C. rigidus-linearis-pinifolius. These three forms apparently constitute a species complex. *C. linearis* was previously reported as having a haploid chromosome number of 11, from two shrubs probably cultivated and of unknown seed source (Smith-White, 1942). This count was checked on the same material, but observations on wild material of the three species resulted in the discovery of triploid, tetraploid, and possibly

Fig. 35. *Kunzia corifolia*. 1-M. Fig. 36. *Callistemon phoeniceus*. 1-M. Figs. 37 and 38. *C. lanceolatus*. 37. 1-M. 38. 2-M. Figs. 39 and 40. *C. pachyphyllus*. 39. 1-M. 40. 2-M. Fig. 41. *C. lilacina*. 2-M. Fig. 42. *C. hortensis*. 1-M. Figs. 43 and 44. *C. acuminatus*. 43. 1-M. 44. 2-M. Figs. 45-47. *C. salignus*. 45. Diakinesis. 46. 1-M. 47. 2-M. Figs. 48 and 49. *C. viminalis*. 48. 1-M. 49. 2-M. Secondary association of 2, 3, or 4 chromosomes are frequent. 50-58. *Callistemon speciosus*. 50. Prometaphase. The shading indicates focus. 51. 1-M. 52. Early 1-A in a flattened cell. Chiasma are incompletely terminalized in some bivalents. 53. 2-M. 54. 2-A, showing simultaneous laggards in the two spindles. 55. Cytomixis between two cells at 2-M. Note how the connecting chromatin has been stretched by the crushing. 56. Cytomixis. Whilst the upper cell is at 2-M, the lower is only at second prophase. The chromatin extruded from the upper to the lower cell is also in a prophase condition. 57. 2-M, showing unequal (13/8) plates, with one chromosome in the cytoplasm. 58. 2-A, showing a persistent first division bridge connecting the two spindles. All \times ca. 2,600.



Text-figs. 59-91.

aneuploid forms with extreme meiotic irregularities, and almost completely aborted pollen. An examination of 12 plants of *C. pinifolius* from Guildford, for example, gave a pollen fertility figure of $1.40 \pm 0.17\%$. In another population, pollen fertility was approximately 25–30% (Plate ii, figs. 24, 25). At the same time, these plants often exhibit a high but variable degree of seed-fertility, and there seems a possibility that they constitute an apomictic species complex. The group is still being studied, and will be dealt with in a subsequent paper.

C. rugulosus. A South Australian species, studied only from cultivated trees in the Sydney Botanic Gardens. Owing to the ease with which hybridization may occur between diploid, sexual species in *Callistemon*, when such are grown in close proximity, such material cannot be considered as representative of the species in nature.

Two cultivated plants of the species were examined. In both the pollen is of very low fertility, ca. 5% (cf. Table 1), almost similar to that found in cultivated forms of *C. lanceolatus* and to that of the apparently apomictic, polyploid species. However, the plants both have the normal haploid number 11, although univalents and meiotic irregularities are frequent. It seems probable that the plants are of hybrid origin, but the condition of the species in nature cannot be indicated.

C. subulatus. Two cultivated plants of this species, also in the Sydney Botanic Gardens, were examined. Chromosome number has not been determined, since the sporogenous tissue in the anthers fails to develop, and mature anthers produce no pollen whatever, good or bad. The consistency of this behaviour has been confirmed on the same two plants on a number of occasions over a period of three years. Capsule fertility, however, is at least 50%, and the species must be suspected as apomictic.

C. salignus. This species, which attains tree size, was studied from wild material in the Coff's Harbour district and from cultivated trees in the neighbourhood of Sydney, where it is often planted in streets and gardens. In all plants examined a high pollen fertility exceeding 90% was found. At diakinesis, 1-M and 2-M (Text-figs. 45, 46, 47), a haploid chromosome number of 11 was determined and meiotic behaviour was quite regular. The species appears to be a normally sexual diploid.

Section Tubuloso-Callistemon Cheel.

In this section the stamens are united in a short ring at the base, a character allied to the five-adelphous stamens of *Melaleuca*.

C. speciosus. A species restricted to Western Australia. The only material available for study was obtained from a plant grown by Mr. E. Cheel at Concord West, near Sydney. This plant forms 11 bivalents at diakinesis and 1-M and is consequently diploid (Text-figs. 50, 51; Plate i, fig. 5). The same number was determined at 2-M and 2-A (Text-fig. 53; Plate i, fig. 6). Squashed early 1-A cells show that the bivalents are held together by either one or two terminal or occasionally subterminal chiasma (Text-fig. 52). Bivalents with submedian chiasma, occasionally present, are frequently late in anaphase separation, and this may be the cause of a certain amount of lagging at late anaphase.

59. *Melaleuca hypericifolia*. 1-M. Fig. 60. *M. elliptica*. 1-M. Figs. 61-71. *M. laterita*. 61. 1-M, normal. 62. 1-M, with four univalents. 63. 1-M, two univalents. 64. 1-M. The cell has been flattened and the chromosomes spread out. There are 14 univalents. 65. Diakinesis. 66 and 67. 1-M plates in side view. The first shows two univalents, placed one at each pole. The other shows four univalents, three being placed towards one pole. 68. 1-A. The 14 univalents are scattered on the spindle. 69. 1-A. Univalents dividing on the spindle at late anaphase. 70. 1-A, showing a chromosome bridge and fragment. 71. 2-M. A case of very unequal plates. Figs. 72 and 74. *M. armillaris*. 72. Prometaphase. 74. 1-M. Fig. 73. *M. alternifolia*. Fig. 75. *Calothamnus villosus*. 1-M. Figs. 76 and 77. *Eucalyptus citriodora*. 76. Metaphase in root tip mitosis. 77. 1-M. Figs. 78 and 79. *E. tetraptera*. 78. 1-M. 79. 2-M. Note the differences in size shown by the chromosomes. Fig. 80. *E. staigeriana*. 1-M. Figs. 81-84. *E. paniculata*. Figs. 81 and 82. Pachytene, showing synzezeis, and the attachment of two chromosome filaments to the nucleolus. 83. Diplotene. 84. Diakinesis. 85. *Syncarpia laurifolia*, 1-M. Fig. 86. *Tristania laurina*. 1-M. Fig. 87. *Backhousia myrtifolia* 1-M. Fig. 88. *Eugenia smithii*. 1-M. Fig. 89. *Eugenia myrtifolia*. 2-M. Fig. 90. *Eugenia leuhmanni*. 1-M. Fig. 91. *Psidium cattleianum*. 2-M. The approximate octoploid condition of this species is probably responsible for the large size of the pollen mother cells. All \times ca. 2,600.

Secondary association is conspicuous, and reaches a maximum of four or possibly five secondary pairs (Plate i, fig. 6; Table 5) at both first and second metaphase. Two abnormalities of behaviour found more frequently in this plant than in any other species examined are worthy of description. At 2-A simultaneous laggards were found in the two spindles. There may be one, two or occasionally more in both spindles (Text-fig. 54; Plate i, fig. 7). In 109 2-A cells, 12, or 11.0%, showed such simultaneous laggards. They probably represent univalent unpaired chromosomes, which have divided at 1-A and which are unable to divide again in the second division, or they may represent cases of misdivision (Darlington, 1939, 1940) of such univalent chromosomes. Cases of laggards in one only of the two spindles were much more rare.

The second abnormality, cytomixis, which was also of frequent occurrence, showed two features which suggest that it is not simply due to damage at the time of fixation, as suggested by Woodworth (1931). Text-fig. 55 shows a case where the PMCs have been separated in crushing. The extruded chromatin, in this case at 2-M, has been stretched out into a long thread, indicating its occurrence prior to the preparation of the slide. Text-fig. 56 shows an observation of greater significance. Whilst cytomixis usually occurs between cells at the same stage of development, and it has been found in all stages from early prophase, first to second telophase, occasionally the connections are between cells in slightly different stages. Text-fig. 56 is such a case. One cell, from which the chromatin has been extruded, is at 2-M, whilst the nuclei in the other cell are in prophase of the second division. It is noteworthy that the intruding chromatin in this cell is also in a prophase condition and not in the metaphase condition of its parent cell. This must mean that the extrusion had occurred before fixation, and that the extruded chromatin had been under the influence of the intruded cell for some time. During the reconstitution of the microspore nuclei, extruded chromatin may be eliminated, leaving them deficient in constitution, and occasionally small supernumerary nuclei were seen at interphase, which were apparently derived from extrusion followed by breakage of the connecting strand.

Unequal partition of the chromosomes to the poles at 1-M, leading to unequal 2-M plates (Text-fig. 57) is apparently a rare occurrence in this plant. The figure shows a distribution of 13/8 in the 2-M plates, with one chromosome extruded in the cytoplasm. A few cases of chromosome bridges at 2-A and of residual first division bridges (Text-fig. 48; Plate i, fig. 8) were also found.

Callistemon viminalis. This species attains tree size and is native to districts in Queensland. It is cultivated extensively as an ornamental and street tree around Sydney, and such cultivated trees have provided material for study.

The haploid chromosome number for the species is 22 (Text-figs. 48, 49; Plate i, fig. 4), and it is thus tetraploid in relation to the basic chromosome number of the genus. Chromosome pairing was quite regular in the plants studied, with normal bivalent formation at 1-M and regular tetrad formation, and the pollen was of good fertility (Table 1; Plate ii, fig. 26). No evidence was found either of failure of chromosome pairing or of multivalent formation, and in its behaviour the species is essentially allotetraploid. The slightly larger size of the pollen, as compared with that of *C. lanceolatus* may be correlated with the polyploidy of the species.

The 1-M and 2-M plates show pronounced secondary association, with frequent groups of three and four, as would be expected in an allopolyploid.

The taxonomic position of *C. viminalis* is a somewhat anomalous one, as it possesses characters which link it with the Series *Callistemonae* of the allied genus *Melaleuca*. Apart from its tree size, it has the filaments of the stamens fused into a short ring, and the structure of the capsules and the differentiation between fertile and infertile seed are characters more typical of *Melaleuca*. The early maturation of the seed, which occurs in 12 months instead of about three years as in other species of *Callistemon*, is also suggestive of *Melaleuca*. On purely morphological grounds, *C. viminalis* could be regarded as a link between the two genera. The suggestion may therefore be made that it is an amphidiploid arising from an intergeneric hybrid, but it is not possible at present to suggest the actual parental species. Its existence

indicates that other amphidiploids might be artificially produced in *Callistemon* and other genera of the tribe.

Melaleuca L. This large genus, of over 100 species, is divided into seven series. Series I of 8 species, which is mainly Western Australian, links the genus with *Callistemon*.

In all ten species studied, representative of four series, a haploid chromosome number of 11 was found, and in all except *M. laterita*, normal chromosome behaviour during meiosis was observed. Illustrated are 1-M plates of *M. hypericifolia* (Text-fig. 59), *M. elliptica* (Text-fig. 60), *M. alternifolia* (Text-fig. 73), and *M. armillaris* (Text-fig. 74; Plate i, fig. 9). Text-fig. 72 illustrates a prometaphase stage in *M. armillaris*, which is typical of all species.

M. laterita. This species is a shrub native to Western Australia which is occasionally cultivated in Sydney. Several plants grown in the Gordon Railway Gardens were studied and in all similar irregularities in chromosome behaviour were observed. Until wild material can be examined, however, this behaviour cannot be accepted as typical of the species.

Chromosome pairing was somewhat irregular, with a tendency to the occurrence of univalents. Typically there were 0-4 univalents (Text-figs. 61-63), but occasionally as many as twelve or fourteen (Text-figs. 64 and 68) were present. An indication of the frequency of univalents is given in Table 4, which is derived from the observation of side views of 1-M plates.

At diakinesis (Text-fig. 65) the univalents are randomly distributed in the nucleus, but at 1-M they tend to lie off the plate, towards the poles of the spindle. At early anaphase they may precede the separating bivalents to the poles (Text-figs. 66-68; Plate i, fig. 10), in which case they remain undivided, or they may return to the equator of the spindle, where they divide into daughter chromatids (Text-fig. 69; Plate i, fig. 11). Their behaviour in this respect would appear to depend on their position at metaphase. A similar behaviour of univalents has been described by Ribbands (1937) and others.

TABLE 4.
Occurrence and Distribution of Univalents at 1-M in Melaleuca laterita.

Number of Univalents.	Distribution.	Number of Cells Observed.
0		50
2	1-0-1	19
	1-1-0	17
	2-0-0	19 57
4	2-0-2	9
	2-1-1	13
	3-0-1	8
	3-1-0	2
	4-0-0	1 33
6	3-0-3	1
	3-1-2	1
	4-0-2	1
	4-1-1	1
	5-0-1	2
	6-0-0	1 7
8	4-1-3	1 1
10		0
12	6-2-4	1 1
14	8-2-4	1 1
Total		148

The failure of chromosome pairing and the irregular behaviour of the univalents result in a number of other irregularities during meiosis. Unequal 2-M plates are frequent, and in extreme cases this inequality may reach the 5/16 distribution shown in Text-fig. 71, in which one chromosome is obscured. Interphase nuclei may be of markedly unequal size, and supernumerary spindles and extruded chromosomes may occur. At second telophase more than the normal four microspore nuclei are frequently formed, resulting in polysporous tetrads and deficient pollen.

Other abnormalities observed include the occasional formation of trivalents, and of chromosome bridges and fragments (Text-fig. 70), indicating the existence of structural hybridity. The cause of the failure of chromosome pairing cannot be exactly defined. Since approximately one-third of the cells at 1-M show complete pairing, members of each chromosome pair must have some segments in common. Any reduction in chiasma frequency, especially where this is normally low as it probably is in Myrtaceae, would lead to the condition described. Such a reduction in chiasma-frequency could be brought about by structural differences between the chromosomes, or by genotypic factors or even environmental causes.

The degree of pollen fertility in the four plants studied, $69.75 \pm 1.34\%$, $95.9 \pm 0.44\%$, $96.5 \pm 0.50\%$ and $99.0 \pm 0.27\%$ respectively, does not show agreement with the extent of meiotic irregularities observed. The breakdown of chromosome pairing, however, is probably considerably affected by environmental conditions, particularly temperature. Mature flowers were collected at the same time as the meiotic stages, during early summer, and cooler weather would be experienced earlier in the year.

Subtribe Beaufortaeae.

This subtribe is entirely restricted to Western Australia, where it comprises five genera. Only one species of the subtribe has been examined.

Calothamnus villosus. Several plants growing in the Sydney Botanic Gardens, and one plant at Gordon, also cultivated, were examined. In all, the haploid chromosome number is 11 (Text-fig. 75), chromosome behaviour is regular, and pollen fertility is high, exceeding 90%.

Subtribe Eucalyptaeae.

This subtribe contains only the genera *Angophora* and *Eucalyptus*. In *Angophora*, the haploid chromosome number for three species is 11 (Smith-White, 1942). In *Eucalyptus*, Atchison (1947) has recently extended the knowledge of chromosome numbers to include 36 species, and all but two of these also have the haploid number of 11. The counts at variance with this, given by Harrison ($n = 14$ for four species) and Sugiura (1936, $2n = 20$ for two species), have been corrected by McAulay and Cruickshank (1937) and by Atchison. There remain two species for which Atchison gives a diploid count of 24, *E. redunca* and *E. corynocalyx*, and it is desirable that these counts should be verified on wild material.

Eucalyptus citriodora. This species is the Lemon-scented gum, native to coastal Queensland, which is frequently cultivated as an ornamental tree and is of particular interest owing to the value of its essential oil. Its chromosome number has previously been reported as $n = 14$ (Harrison, 1934) and $n = 10$ (Sugiura, 1936), but Atchison (1947) recently recorded a diploid count of 22. Present data are derived from cultivated trees at Sydney Botanic Gardens, at Grafton and in suburban gardens. A count of $2n = 22$ was obtained in sections of root tips of germinating seeds, fixed in 2BE and stained in iodine-gentian violet (Text-fig. 76). The chromosomes are small, and often crowded, and a miscount giving a diploid number of 20, as obtained by Sugiura, could easily be made. The somatic chromosomes are about 1-1.5 microns in length, and in the slides examined no conspicuous morphological features could be determined.

In microsporogenesis, haploid counts of $n = 11$ were also obtained at 1-M (Text-fig. 77) and at other stages. In the material studied, chromosome behaviour during meiosis was quite regular, and pollen fertility was high.

Eucalyptus tetraptera. A dwarf mallee from Western Australia. Material was obtained from a single plant in the Sydney Botanic Gardens.

The species, although of dwarf habit, possesses many characters suggestive of gigantism, as for example in the large, thick, almost fleshy leaves, and the very large buds, flowers, anthers and fruits characteristic of a number of Western Australian species of "mallees". The haploid chromosome number, however, is the same as that of other Eucalypts, 11, and the meiosis is entirely regular. Thus in over one thousand 1-M plates and some 500 2-M and 2-A cells, no irregularities were observed.

The bivalent chromosomes at 1-M are larger than usual (Text-fig. 78; Plate i, fig. 12), conforming with the morphological gigantism of the plant, and show conspicuous differences in size, a difference also observable at 2-M (Text-fig. 79). Secondary association both at 1-M and 2-M is marked, and has been analysed in some detail (Table 5). A considerable proportion of cells show the maximum association of five pairs, and this association can be seen to be between chromosomes of like size. One chromosome, the largest of the set, is never associated in any secondary group. This condition is similar to that observed in *Calythrix* (Smith-White, unpublished).

Eucalyptus staigeriana. This species, native to the far north of Queensland, was studied from trees grown in Sydney from seed supplied by the Queensland Forest Service. In the more southern latitude the trees do not thrive, but they can be maintained in sheltered situations. The two trees studied, flowered when only 3 feet high and 3 years of age. The haploid chromosome number is 11 (Text-fig. 80), and except for the occurrence of secondary association, meiosis is regular. Pollen has not been examined, but in 1946 a capsule set of under 10% was obtained. This infertility, however, may be due to climatic effects.

E. paniculata. This is the grey or white ironbark of eastern Australia. The chromosome number of the species was given in a previous paper (Smith-White, 1942). Some observations on prophase development in microsporogenesis, and on chiasma frequency are reported here. Broadly the prophase development follows that to be described for *Chamaelaucium* (Smith-White, unpublished). Pachytene is of long duration, and during this stage, and particularly where synezeisis is pronounced, two chromosome strands can usually be seen attached to the nucleolus (Text-figs. 81, 82; Plate i, fig. 14). This condition indicates that two nucleolar organizing chromosomes are present, and suggests that the chromosome complement is a secondarily balanced one. The large and conspicuous pycnotic granules associated with the nucleolus in *Chamaelaucium*, and particularly in *Darwinia*, are not seen in this species. Only a single large nucleolus is present at prophase, but with the tendency of multiple nucleoli to fuse, this would almost certainly occur during the previous telophase.

The condition of synezeisis at pachytene may be very pronounced, and from its mode of occurrence it would appear to have some significance.

Following pachytene the chromosomes contract rapidly, and at diplotene, when the repulsion between the two chromosomes of each bivalent is strong, and their free parts are widely divergent, it is possible to get some idea of chiasma frequency. This varies from 1 to 3 per bivalent, and the chiasma may be either terminal, subterminal or interstitial. In the cell figured (Text-fig. 83) there are approximately 24 chiasmata, or an average of 2.18 per bivalent. Of these, 15 are terminal. It is probable that the process of terminalization commenced earlier, and that some of the chiasmata have been already cancelled out. This process of terminalization is continued to diakinesis (Text-fig. 84; Plate i, fig. 15), and simultaneously there is a further contraction of the bivalents. At this stage the bivalents have attained maximum contraction, and are arranged uniformly spaced near the surface of the nucleus. Any determination of chiasma conditions is then difficult, and can only be attempted in squash preparations which have been flattened considerably.

An average frequency of little more than two chiasmata per bivalent seems to be characteristic of this species, and of other genera and species of the Myrtaceae. Consequently any factors which tend to disturb or lower chiasma frequency, whether they be structural, genetical or physiological, would easily lead to a considerable frequency of univalents, a disturbance of the whole meiotic process, and a high proportion of infertile pollen, such as has been observed in species of *Melaleuca*, *Leptospermum* and *Callistemon*.

E. dives Sch. The chromosome number in this species has been reported previously (Smith-White, 1942). Examination of a number of trees of the species has confirmed this count, but pollen fertility has been found to show considerable variation. In four plants, the degree of pollen fertility was 0%, $50.1 \pm 2.72\%$, $53.0 \pm 1.93\%$ and $69.0 \pm 1.34\%$. The species requires further study from this aspect.

Subtribe Metrosiderae.

This, the fifth subtribe of the Leptospermeae, differs from all the other subtribes in its geographical distribution. With a centre of diversity in South-east Asia and Indonesia instead of Western Australia, it extends to the east coast of Australia, Polynesia, and America. It is quite unrepresented in Western Australia, and the eastern species are intrusions from the Malayan-Indonesian flora and are characteristic mesophytes of the rain-forest areas.

The chromosome numbers in *Tristania conferta* and *Backhousia citriodora* were reported previously (Smith-White, 1942). The following additional species have since been studied: *Syncarpia laurifolia*, *Tristania laurina*, *Backhousia myrtifolia*.

In all three species the haploid chromosome number is 11 (Text-figs. 85, 86, 87), chromosome behaviour is regular, and the pollen is of high fertility.

TRIBE MYRTOIDEAE.

This tribe is essentially tropical in nature, with its main centre of diversity in Central and South America, and a secondary centre in tropical south-eastern Asia. It extends across Asia, and a single species, *Myrtus communis*, reaches the Mediterranean. It intrudes, with the Malayan-Indonesian flora, into the eastern humid zone of Australia, but is entirely absent from other parts of the Continent.

The chromosome number of several exotic species has been previously reported (Atchison, 1947). In *Myrtus communis* (Greco, 1930), *Feijoa sellowiana* (Bowden, 1945), and *Eugenia* spp. (Pijl, 1934), the chromosome number is $n = 11$, although in *Eugenia jambosa* polyploid forms apparently exist. In this subfamily the basic chromosome number 11, agrees with that found in the Leptospermoideae.

Eugenia. A large genus, of nearly 1,000 species, predominantly American. Most of the Australian species are endemic, as are the three species reported in the present paper. *E. smithii*, the well-known Lilli-pilli, is the most southern in range in the whole tribe. All three species show a haploid chromosome number of 22 (Text-figs. 88, 89, 90), and they are thus tetraploid with respect to the normal number in the family. They also show quite regular meiotic behaviour, and the few trees examined possess high pollen fertility.

It has been shown clearly by various authors (Stebbins, 1940; Babcock, 1942; Manton, 1937) that in any group in which diploid and tetraploid species or forms occur, the polyploids often show a much wider distribution than the diploids, or occur predominantly on the borders of the distribution of the group. The polyploids often show a greater tolerance of more extreme or adverse conditions than do the diploids. Thus the polyploidy of these Australian species of *Eugenia* conforms with the assumption that the centre of origin of the genus, and of the whole tribe, has been in tropical America, where the centre of diversity is also found.

Psidium. This is an extra-Australian genus. A tree of the Brazilian *P. cattleianum*, growing in the Sydney Botanic Gardens, has been examined, and is of interest because of its high polyploidy. It has a haploid chromosome number of ca. 40-44, and is consequently octoploid or approximately so (Text-fig. 91). Chromosome behaviour, however, appears to be regular, and the pollen mother cells are notable chiefly for their large size and the width of the meiotic spindles. Atchison (1947) has shown that this high number is found in several species of the genus, although other species are diploids.

DISCUSSION.

SECONDARY ASSOCIATION AND THE BASIC CHROMOSOME NUMBER OF THE MYRTACEAE.

Table 5 gives a collection of data for a number of genera and species of the Leptospermoideae, in regard to the occurrence of secondary association. Only those

species with the normal haploid number of 11 have been included in this table, and the data have been assembled for the most part from drawings of 1-M and 2-M plates. In the case of *Leptospermum flavescens*, *C. speciosus* and *Eucalyptus tetraptera* and a few other species, however, this secondary association has been studied directly. In scoring secondary groupings, the practice of Alam (1936) has been followed, groups of three being scored as equivalent to two secondary pairs. The data indicate that secondary association is of frequent occurrence throughout the family, and that it reaches a maximum of five secondary pairs, with a mean of three pairs. In no case have the chromosomes been associated into less than six separate groups.

TABLE 5.
Summary of Secondary Association in the Leptospermoideae.

Species.	Number of Secondary Associations.						Total.
	0	1	2	3	4	5	
<i>Baeckea diffusa</i>					3	4	7
„ <i>densifolia</i>	1	1	1				3
<i>Leptospermum laevigatum</i> ..		2	2				4
„ <i>flavescens</i>		3	8	16	8	2	37
„ <i>citratum</i>	1	2					3
„ „ Var. A			2	7	9	6	24
„ <i>grandifolium</i>			2	1	5		8
„ <i>stellatum</i>			2				2
„ <i>rotundifolium</i>				1		1	2
<i>Kunzia corifolia</i>		1	1	1			3
<i>Callistemon lanceolatus</i> ..	1	2	2				5
„ <i>pachyphyllus</i>			1	1			2
„ <i>lilacina</i>				1	1		2
„ <i>acuminatus</i>	2	1		1	1		5
„ <i>salignus</i>	1	1	1	1			4
„ <i>speciosus</i>		9	12	18	12		51
<i>Melaleuca laterita</i>	1	2	5	1	1		10
„ <i>hypericifolia</i>	2	1					3
„ <i>armillaris</i>		1	1				2
<i>Calothamnus villosus</i>			2	2	1		5
<i>Eucalyptus ficifolia</i>	2	1	2	3	5	1	14
„ <i>gummifera</i>	1	1	3	1	1		7
„ <i>haemastoma</i>			1	1	2		3
„ <i>dives</i>		2	2	3	2		9
„ <i>incrassata</i>			1	1	1	1	4
„ <i>tetraptera</i>		5	15	36	44	26	126
„ <i>staigeriana</i>		1	1	6	14	3	25
Total	14	39	72	111	115	45	396

McAulay and Cruickshank (1937) first drew attention to the occurrence of secondary association in the Myrtaceae in *Eucalyptus Johnstoni*. Smith-White (1942), on the basis of a preliminary study of the phenomenon in several genera, suggested that the chromosome complement of 11 would be found to be a secondarily derived one, possibly from the number 7, and that consequently the species studied were in fact secondary polyploids.

The significance of secondary association in the Myrtaceae will be discussed in more detail in a subsequent paper. Since its recognition by Darlington (1928), its occurrence has been used, with or without supporting evidence, to establish the secondarily derived nature of the chromosome complements in many groups of plants, notably in the Subfamily Pomoideae of the Rosaceae by Darlington and Moffett (1930) and Moffett (1931), and also in *Dahlia* (Lawrence, 1931), *Oryza* (Nandi, 1936), *Brassica* (Catcheside, 1934) and the Cruciferae (Alam, 1936), *Cicer* (Iyengar, 1939) and many other cases. It has been shown that it is the maximum rather than the most frequent degree of secondary association which is significant, and the data presented for the Myrtaceae indicate that the basic chromosome complement of 11, common to the Leptospermoideae

and Myrtoideae has been derived from a primitive set of six chromosomes, rather than of seven as previously suggested.

In the present paper some additional supporting evidence for this conclusion has been presented. In a study of the prophase development in *Eucalyptus paniculata*, two chromosome stands were fairly constantly seen attached to the single nucleolus at pachytene. Since McClintock (1934) showed the relationship between the formation of nucleoli and the presence of nucleolar organizing bodies on particular chromosomes, many workers have demonstrated the significance of this relationship, and the subject has been reviewed at length by Gates (1942). In *E. paniculata* there are apparently two nucleolar-organizing bodies situated on two different chromosomes. Owing to their liability to fusion, two separate nucleoli would not be expected during prophase, but careful observation might demonstrate their initial formation at late telophase, particularly following the first meiotic division.

THE STATUS OF SPECIES IN THE MYRTACEAE.

Babcock (1942) and his co-workers have shown the nature of the evolutionary processes operating in the genus *Crepis*. These, comprising gene mutation, structural alteration, hybridization, polyploidy, and apomixis, are not of equal importance, and their relative importance may differ considerably in different groups of plants. Darlington (1932) has outlined the nature of species in relation to their internal structure, and has described six kinds of species. In the Myrtaceae, the majority of the species studied belong to Darlington's first kind, i.e., they are simple diploid species, sexually reproducing and with regular meiosis. Attention must be drawn here to the data presented by Lawson (1930), dealing with pollen fertility in several species of *Leptospermum* and *Callistemon*, which in some cases show a serious discrepancy with similar data for the same species presented here. The source of Lawson's material is not known, but in part it may have been from cultivated material. For the characterization of any species in regard to pollen fertility, it is apparent that a fairly large number of individual plants should be examined, and that the use of cultivated material is dangerous, especially where closely related species are cultivated together.

From the occurrence, although usually rarely, of chromosome bridges in most of the species studied, it is apparent that structural change has played some part in speciation within the family, but gene mutation has probably been a more important factor.

Darlington's second type is the polyploid species. A few examples of normally sexual allopolyploid species are found, and in one case at least, *Callistemon viminalis*, the available evidence suggests an amphidiploid origin.

The third type, the mixed species, is represented by the *Callistemon rigidus-linearis-pinifolius* complex, but since this group is apparently apomictic, it is more properly placed in the sixth class, of clonal species. As is usual in clonal groups, this complex is characterized by great uniformity within the species or microspecies, and by slight but constant differences between the species. Darlington's fourth and fifth types, sex-heterozygote and complex heterozygote species, are not represented in the family.

SUMMARY.

Previous records of chromosome numbers in the Myrtaceae are reviewed. It is indicated that reports of haploid numbers of 10 and 14 are probably erroneous.

Chromosome numbers are reported for 13 genera and 63 species, including 3 varieties, and representative of all taxonomic subdivisions of the Leptospermoideae and Myrtoideae. Of these 55 species are reported for the first time. The great majority of these species are normal diploids, with a haploid chromosome set of 11.

The evidence of secondary association has been analysed, and, together with some supporting evidence of prophase behaviour in *Eucalyptus*, indicates that the basic set of 11 is a derived one, probably from an original primitive set of six. Secondary polyploidy has operated at some early stage in the evolution of the family.

The nature of species within the family is discussed. Most species show evidences of structural chromosomal changes giving rise to rare chromosome bridges. Such

limited structural hybridity, together with genetical and physiological causes, probably conditions a reduction in chiasma frequency, leading to univalent formation in certain species. This would be more marked owing to the already low chiasma frequency characteristic of the family.

Polyploidy has been responsible only for a very limited degree of speciation. Five regularly behaving tetraploids are reported, but three of these are in the one genus, *Eugenia*. Of the other two, one is presumptively an intergeneric amphidiploid hybrid.

It is possible that the polyploidy found in the three species of *Eugenia* studied is associated with the fact that they occur at one extreme limit of the world distribution of that large genus.

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EXPLANATION OF PLATES I AND II.

PLATE I. CYTOLOGY OF THE MYRTACEAE.

- Fig. 1. *L. parvifolium*, 2-M, $n = 22$.
- Fig. 2. *C. acuminatus*, 1-M, $n = 11$.
- Fig. 3. *C. acuminatus*, 2-M.
- Fig. 4. *C. viminalis*, 1-M, $n = 22$.
- Fig. 5. *C. speciosus*, 1-M, $n = 11$.
- Fig. 6. *C. speciosus*, 2-A.
- Fig. 7. *C. speciosus*, showing simultaneous laggards.
- Fig. 8. *C. speciosus*, 2nd Division bridge.
- Fig. 9. *M. armillaris*, 1-M, $n = 11$.
- Fig. 10. *M. laterita*, 1-M, showing two univalents, $n = 11$.
- Fig. 11. *M. laterita*, 1-A, with dividing univalent.
- Fig. 12. *E. tetraptera*, 1-M, $n = 11$.
- Fig. 13. *E. paniculata*. Early prophase.
- Fig. 14. *E. paniculata*, Pachytene. The same cell drawn in Text-fig. 81.
- Fig. 15. *E. paniculata*, Diakinesis.
- Fig. 16. *E. paniculata*, 1-M, $n = 11$.

Photographs $\times 2,000$.

PLATE II. POLLEN OF THE MYRTACEAE.

- Fig. 1. *Agonis flexuosa*. The empty pollen has not shown up well in the photograph.
- Fig. 2. *L. flavescens*. The pollen of wild plants is uniformly good.
- Fig. 3. *L. lanigerum*. Pollen size of this diploid species should be compared with that of *L. parvifolium*.
- Fig. 4. *L. parvifolium*. The pollen of this tetraploid species is distinctly larger than that of its diploid allies.
- Fig. 5. *L. stellatum*. Pollen of a plant with about 40% fertile pollen.
- Fig. 6. *C. lanceolatus*. Pollen of wild plants is usually of high fertility.
- Fig. 7. *C. lanceolatus*, hort. Low pollen fertility is frequent in cultivated material.
- Fig. 8. *C. linearis*. Pollen of a plant from Fairfield, with about 1% fertile pollen.
- Fig. 9. *C. linearis*. Pollen of a green flowered form from National Park.
- Fig. 10. *C. viminalis*. Pollen of this tetraploid species is only little larger than that of its diploid allies.
- Fig. 11. *M. laterita*. Pollen of a plant showing 69% of fertile pollen.
- Fig. 12. *E. dives*. The empty pollen is conspicuous. The plant had 50% fertile pollen.

All photographs \times ca. 240.

A SURVEY OF CHROMOSOME NUMBERS IN THE EPACRIDACEAE.

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(Plates iii and iv; eighty Text-figures.)

[Read 31st March, 1948.]

INTRODUCTION.

The Epacridaceae is essentially an Australian family of heaths, where it takes the place in an ecological sense of the Ericaceae of South Africa and other parts of the world. It contains no species of direct economic importance, but many have been cultivated as hothouse plants in England, particularly during the nineteenth century. It claims an important place in the floristics and ecology of the Australian flora.

The family contains some 30 genera and about 400 species, (Willis, 1925), mainly Australian, but with a few genera extending to New Zealand, New Caledonia and Malaya, and one monotypic genus is endemic to Patagonia. Systemmatically the family is placed in the Order Ericales, together with the Ericaceae (80 genera, 1500 species), the Clethraceae (1/30), the Pyrolaceae (10/30) and the Diapensiaceae (6/12), (Rendle 1938), and the Order is undoubtedly a very natural one. Generally the Epacridaceae has been considered an advanced and specialised group derived from the Ericaceae (Rendle 1938), showing progressive evolution in gamopetally, epipetally, anther dehiscence, and other characters, and in fact two monotypic genera, *Prinotes* (Tasmania) and *Lebetanthus* (Patagonia) closely approach the Ericaceae, and might be regarded as links between the two families.

Whilst the Ericaceae has been studied cytologically, by several workers (e.g. Hagerup 1928, Longley 1927, Sax 1930), the only reference to the chromosomes of a species of the Epacridaceae is in the work of Samuelson (1913), and since no other references are given by Darlington and Janaki Ammal (1944) or by Tischler (1927, 1931, 1936, 1937, 1938), it seems that the family has been neglected from this aspect.

TAXONOMY OF THE EPACRIDACEAE.

The family has been divided into two tribes or subfamilies (Bentham 1869, Bentham and Hooker 1876), the Styphelieae and Epacrideae, which are quite distinct, the Epacrideae containing genera with capsular fruits, whilst those with indehiscent, usually succulent fruits are placed in the Styphelieae. Drude constituted a third tribe to include the two anomalous genera *Prinotes* and *Lebetanthus*. Morphologically, the Epacrideae is more closely allied to the Ericaceae, and might in consequence be considered as the more primitive tribe. In the Styphelieae there has been a considerable difference of opinion amongst leading taxonomic authorities as to the status of the various genera. Robert Brown established 16 genera on the basis of his descriptive and exploratory work, but Sprengel accepted only the single genus *Styphelia*. Von Mueller (1868) grouped most of Brown's genera into *Styphelia*, but retained the same groups at the sectional level. Bentham (1869) did not accept Mueller's classification, apparently for the sake of convenience. Later Drude (in Engler and Prantl 1889) followed Mueller, with minor alterations, and this last classification was accepted by Maiden (1916).

The Australian distribution of the Tribes Styphelieae and Epacrideae is given in Table 1, which has been prepared from Bentham's Flora Australiensis (1869) and from the Floras of several States, by Bailey (1909), Maiden (1916), Ewart (1930) and Black (1926). It is not claimed that the list is complete, but the total number of

Australian species would not exceed 350. Several important facts emerge from a study of the table. One is the small size of most of the genera. *Leucopogon*, with about 130 species, is the only one of any considerable size, and only four other genera exceed ten species each. The second striking fact is that of the 26 genera and 317 species listed, only 8 genera and 12 species are common to Eastern and Western Australia, suggesting that the two floras have been isolated for a long period of time, or that speciation has been rapid. The genera endemic to Western Australia are usually specialized relatives of Eastern ones, and the data do not suggest Western Australia as the source of the whole group, as seems to be the case in the Myrtaceae and some other families.

TABLE I.
Australian Distribution of the Epacridaceae.

Genus.	Q.	N.S.W.	V.	T.	S.A.	Total Eastern Species.	W.A.	Total Species.
<i>Styphelia</i>	1	6	1	1	1	8	5	13
<i>Coleanthera</i>	—	—	—	—	—	—	3	3
<i>Astroloma</i>	—	3	3	2	2	3	16	18
<i>Conostephium</i>	—	—	—	—	—	—	7	7
<i>Melichrus</i>	2	2	1	—	—	2	—	2
<i>Pentachondra</i>	—	—	1	4	—	4	—	4
<i>Trochocarpa</i>	2	1	1	3	—	6	1	7
<i>Cyathodes</i>	—	—	1	8	—	8	—	8
<i>Brachyloma</i>	2	2	4	3	2	5	2	7
<i>Needhamia</i>	—	—	—	—	—	—	1	1
<i>Lissanthe</i>	—	2	2	2	1	3	—	3
<i>Leucopogon</i>	16	27	16	11	11	47	92	135
<i>Acrotiche</i>	2	3	3	1	6	9	3	10
<i>Monotoea</i>	3	3	3	4	—	7	1	8
<i>Oligarrhena</i>	—	—	—	—	—	—	1	1
<i>Choristemon</i>	—	—	1	—	—	1	—	1
Total Styphelieae	28	49	37	39	23	103	132	228
<i>Epacris</i>	3	18	13	11	1	32	—	32
<i>Lysinema</i>	1	1	—	—	—	1	6	7
<i>Rupicola</i>	2	—	—	—	—	2	—	2
<i>Archeria</i>	—	—	—	3	—	3	—	3
<i>Prionotes</i>	—	—	—	1	—	1	—	1
<i>Cosmelia</i>	—	—	—	—	—	—	1	1
<i>Sprengelia</i>	1	3	1	1	1	3	—	3
<i>Andersonia</i>	—	—	—	—	—	—	21	21
<i>Richea</i>	—	1	1	9	—	9	—	9
<i>Dracophyllum</i>	1	1	—	2	—	4	6	10
Total Epacrideae ..	8	24	15	27	2	55	34	89
Total Epacridaceae	36	73	52	66	25	158	166	317

MATERIALS AND METHODS.

The genera and species for which data are presented in this paper are all native heaths found growing within reasonable access of Sydney. A summary of the species is given in Table 2.

Microsporogenesis was studied in squash preparations fixed in 1:3 acetic-alcohol for 12–24 hours, and squashed on the slide in iron acetocarmine. Any maceration of the anthers was not found desirable. The preparations were usually made permanent in Euparal, after floating off the covers in acetic-alcohol. Any tendency to overstaining was corrected by a brief treatment in alcohol acidified with 0.1% HCl. Slides prepared after Feulgen staining did not give such satisfactory results as had been obtained with the Myrtaceae and Rutaceae.

Diploid counts at metaphase of somatic mitosis were obtained from young ovary and ovule tissue and from very young leaves, which were fixed in aceto-alcohol, macerated

on the slide in acidified aceto-lacmoid (cf. Darlington and La Cour, 1942), and squashed in aceto-lacmoid.

Drawings were made with an Abbe camera lucida, at an initial magnification of $\times 3,900$, and are reproduced at a magnification of $\times 2,600$, except where otherwise indicated.

TABLE 2.
Chromosome Data for the Epacridaceae.

Species.	Localities.	No. of Plants Examined.	Chromosome No.		Availability of Meiotic Material.	Pollen Develop- ment.
			Haploid.	Diploid.		
<i>Styphelia longifolia</i> R.Br. ..	Gordon.	5	4	8	March-July.	S*
" <i>laeta</i> R.Br. ..	La Perouse.	2	4	—	March.	S
" <i>triflora</i> Andr. ..	Nat. Park.	10	4	8	March-July.	S
" <i>viridis</i> Andr. ..	La Perouse.	3	4	—	March.	S
" <i>tubiflora</i> Sm. ..	Gordon ; Nat. Pk.	4	4	—	Jan.-March.	S
<i>Astroloma humifusum</i> R.Br. ..	Nat. Pk. ; Fairfield.	3	—	24	—	S
" <i>pinifolium</i> Benth. ..	Nat. Pk. ; La Perouse.	10	7	14	Feb.-April.	T
<i>Melichrus rotatus</i> R.Br. ..	Lane Cove R.	2	8	16	May-June.	S
" <i>urceolatus</i> R.Br. ..	Albury.	3	8	—	June.	S
<i>Trochocarpa laurina</i> R.Br. ..	Nat. Pk.	2	10	—	Feb.-April.	T
<i>Brachyloma daphnoides</i> Benth. ..	Albury ; Lane Cove R.	4	9	18	June-August.	T
<i>Lissanthe sapida</i> R.Br. ..	Springwood.	3	—	14	—	—
" <i>strigosa</i> R.Br. ..	Yagoona ; Fairfield.	4	7	—	May-June.	T
<i>Leucopouon amplexicaulis</i> R.Br. ..	Nat. Pk. ; Kuring- gai.	3	12	—	April-May.	S
" <i>lanceolatus</i> R.Br. ..	Lane Cove ; Oberon.	5	24	—	May-June.	S
" <i>microphyllus</i> R.Br. ..	Gordon ; Nat. Pk.	4	6	12	March-May.	S
" <i>virgatus</i> R.Br. ..	Albury.	2	10	20	June.	T
" <i>ericoides</i> R.Br. ..	Lane Cove R. ; La Perouse.	4	6	12	March-April.	S
" <i>esquamatus</i> R.Br. ..	Lane Cove ; La Perouse.	5	4	8	March-April.	S
" <i>setiger</i> R.Br. ..	Lane Cove R.	4	4	8	March.	S
" <i>juniperinus</i> R.Br. ..	Lane Cove R. ; Gordon.	12	4 II + 4 I	12	March-April.	S
" <i>appressus</i> R.Br. ..	Gordon.	2	6	—	March-April.	S
<i>Acrotriche divaricata</i> R.Br. ..	Springwood.	2	—	18	—	—
" <i>serrulata</i> R.Br. ..	Albury.	2	9	—	June.	T
<i>Monotoca elliptica</i> R.Br. ..	Narrabeen.	3	12	24	May-June.	S
" <i>scoparia</i> R.Br. ..	Gordon ; Lane Cove R.	4	12	—	April-May.	S
<i>Epacris longiflora</i> Cav. ..	Gordon.	3	13	—	March-May.	T
" <i>reclinata</i> Cunn. ..	Blackheath.	1	13	—	May.	T
" <i>crassifolia</i> R.Br. ..	Springwood.	2	13	—	May.	T
" <i>obtusifolia</i> Sm. ..	King's Tableland.	2	13	—	May.	T
" <i>paludosa</i> R.Br. ..	King's Tableland.	2	13	—	April-May.	T
" <i>microphylla</i> R.Br. ..	Lane Cove ; Kuring- gai.	3	13	—	April-June.	T
" <i>pulchella</i> Cav. ..	Gordon.	4	13	—	March-April.	T
<i>Lysinema pungens</i> R.Br. ..	Gordon.	4	13	—	March-May.	T
<i>Sprengelia incarnata</i> Sm. ..	Kuring-gai ; Nat. Pk.	3	12	—	May-June.	T
<i>Dracophyllum secunatum</i> R.Br. ..	Lane Cove R.	3	13	—	May.	T

*S = *Styphelia* type.

T = Tetrad type.

CYTOLOGY OF THE GENERA AND SPECIES.

TRIBE STYPHELIEAE.














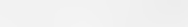
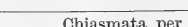
1. *Styphelia* Sm. This genus of about 13 species is divided into two sections, *Eustyphelia* and *Soleniscia*. The latter is restricted to Western Australia, and has not been studied.

The five eastern species studied, all belonging to *Eustypheia*, have a haploid chromosome number of 4. In *S. longifolia* and *S. triflora*, the diploid number determined from ovule crushes is 8, and all chromosomes are of approximately equal length (2.7-3.0 μ), and all show median or submedian constrictions (Text-figs. 1, 8; Plate iii, fig. 1). In *S. longifolia* one pair of chromosomes show a long and pronounced constriction region.

In *S. longifolia* the course of meiosis in the pollen mother cells is normal. The resting mother cell is of the vesicular type, and contains a large nucleolus with a conspicuous pycnotic body attached to it, this body being probably homologous with a heterochromatic region of a nucleolar organizing chromosome. At diplotene and diakinesis the chiasma frequency is high, with two, three or sometimes four chiasmata per bivalent (Text-figs. 2, 3). The chiasmata may occur at various points along the chromosome arms, on both sides of the centromeres. By the time of late diakinesis and 1-M, partial terminalization is evident, giving "ring" or sometimes "rod" bivalents (Text-fig. 5). In polar view at 1-M, the bivalents appear as more or less oval bodies 1.8-2.0 μ in length (Text-fig. 4). Interphase and the second division as far as telophase also appear to be normal. At 2-M the chromosomes are rod-shaped, ca. 2.0 microns in length, and show the typical repulsion between the chromatid arms (Text-figs. 6, 7).

In *S. triflora* the bivalents at 1-M are similar (Text-fig. 9; Plate iii, fig. 2), but in side views analysis of the chiasma-relationships of the chromosomes may be very clear (Text-figs. 10, 11). Table 3 shows the chiasma relationships of 15 cells at this stage. Of the 60 bivalents, 53 showed the "ring" form, with chiasmata on both sides of the centromere, and the mean chiasma-frequency is 3.08 ± 0.02 per bivalent. This high chiasma-frequency appears to be typical of all the 4-chromosome species of *Stypheia* and *Leucopogon*, and is of special significance in *Leucopogon juniperinus* (Smith-White, 1948). At 2-M the chromosomes of *S. triflora* remain less contracted than in *S. longifolia* (Text-figs. 12, 13; Plate iii, fig. 3), and may measure 3 microns in length. As a consequence of the lesser contraction, the chromatid arms are sometimes widely divergent.

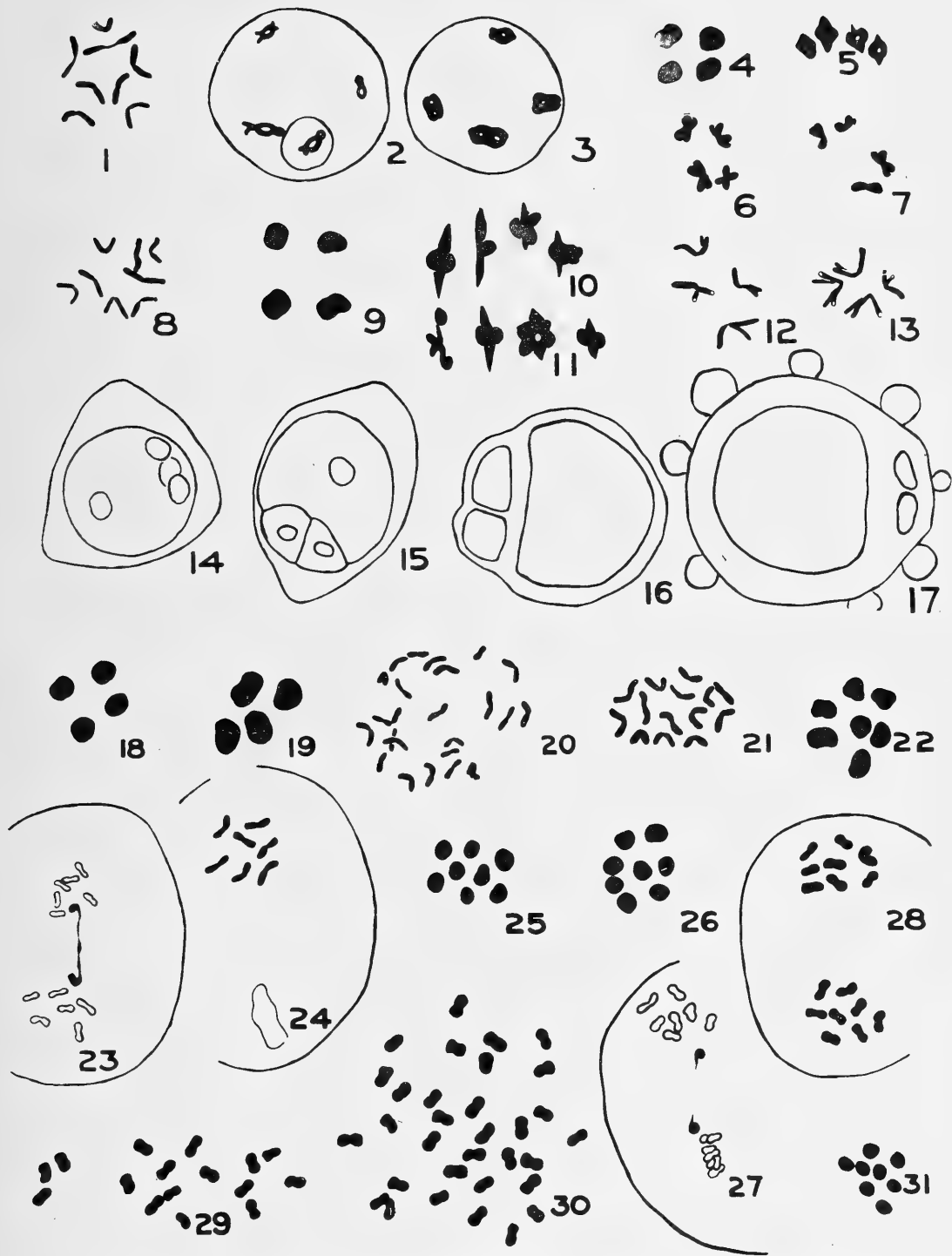
TABLE 3.
Analysis of Chiasma at 1-A in *S. triflora*.

Cell No.	Chiasma Diagrams.	No. of Chiasmata.		Total Chiasmata.
		Terminal.	Interstitial.	
1		8	6	14
2		4	7	11
3		4	7	11
4		7	5	12
5		8	6	14
6		3	6	9
7		6	8	14
8		6	6	12
9		5	7	12
10		6	5	11
11		7	6	13
12		7	6	13
13		7	5	12
14		3	9	12
15		8	7	15
Total ..		89	96	185

Chiasmata per cell, 12.33.

„ per bivalent, 3.08 ± 0.015 .

The chromosomes of the other species are similar. Illustrated are 1-M chromosomes of *S. viridis* and *S. tubiflora* (Text-figs. 18, 19).



Text-figs. 1-31.

1-7. *Styphelia longifolia*. 1. Mitotic chromosomes in ovule tissue. 2. Early diakinesis in a pollen mother cell. 3. Late diakinesis. 4. First metaphase. 5. First metaphase in side view to show the chiasma relations of the bivalents. 6. and 7. Second metaphase, the two plates from the same pollen mother cell. 8-17. *Styphelia triflora*. 8. Mitotic chromosomes in ovule tissue.

Legend continued on page 42.

The sequence of stages in pollen development in *Styphelia* is peculiar, if not unique, and has been designated the "styphelia" or "S" type to distinguish it from the "tetrad" or "T" type typical of the tribe Epacridae, of the Ericaceae, and of the Ericales generally. Search has not discovered any account of the method of development, which merits a fairly detailed description.

The newly formed microspore nuclei are at first uniformly placed, either tetrahedrally or quadrantly, in the mother cell, but prior to any division of the cytoplasm three of the nuclei migrate to one end of the cell, leaving one nucleus isolated at the other (Text-fig. 14; Plate iv, fig. 29). Cell walls are then laid down, dividing the old pollen mother cell unequally into one large and three small cells, each with a microspore nucleus (Text-fig. 15; Plate iv, fig. 30). There is, however, no obvious difference or inequality between the four microspore nuclei which could suggest any cytological or gross chromosome basis for this unequal behaviour. The subsequent growth is entirely of the large microspore, the three smaller ones taking on a role analogous to the polar bodies in animal oogenesis. With the growth of the functional microspore, and the pronounced thickening of the cell wall of the pollen grain, the three non-functional microspores gradually become squashed out of existence (Text-figs. 16, 17; Plate iv, fig. 31). The mature pollen grain is apparently single, as described by Brough (1924), in which the non-functional cells cannot be distinguished. Even in mature anthers, however, pollen grains which have died at an earlier stage of development through cytological or genetical unbalance, or through other causes, still show the original tetrad nature of the pollen.

The question of the origin of this peculiar method of pollen development, and of its significance in relation to cytological conditions in some species of the Styphelieae, will be dealt with at a later stage of the present paper.

2. *Astroloma* R. Br. A genus of about 18-20 species which was divided by Bentham and Hooker into three sections. Only three species occur in New South Wales, one from each of the three sections, but one of these, *A. conostephioides* F.v.M. of the section Pentataphrus, is southern and inland in occurrence, and has not been available.

Astroloma humifusum. (Section Stomarrhena.) Up to the present meiotic stages have not been found in this abundant species, but at mitotic metaphase in crushes of young ovules, a diploid count of 24 was obtained (Text-fig. 20). The species is thus hexaploid in relation to the chromosome number of the allied genus *Styphelia*.

Mature pollen is of the "single" type, and the method of pollen development is similar to that described for *Styphelia*.

Astroloma pinifolium. (Section Stenanthera.) This species was studied from localities at La Perouse and at Audley, National Park. The species has a diploid chromosome number of 14, and is in marked contrast to *A. humifusum*. The chromosomes at mitotic metaphase (Text-fig. 21) are similar to, but slightly smaller than those of *Styphelia longifolia*.

During meiosis in the pollen mother cells, seven bivalents are formed at 1-M (Text-fig. 22) and 2-M plates of seven chromosomes are also usual (Text-fig. 24; Plate iii, fig. 4). Although no evidence of the occurrence of univalents was detected in the plants studied, and the frequency of laggards or of chromosome bridges was low (Text-fig. 23; Plate iii, fig. 5), under 1%, a considerable degree of polyspory in the young tetrads of one plant was observed. In these, microcytes were frequent, and only $56.5 \pm 1.4\%$ of the tetrads had the normal number of four microspores. This behaviour may be responsible for the high degree of pollen failure, and the unusual appearance of the pollen, characteristic of the species.

Continuation of legend from page 41.

9. First metaphase. 10 and 11. First metaphase in side view, showing the chiasma relations in the bivalents. 12, 13. Second metaphase, the two plates from the same pollen mother cell. 14-17 ($\times 1,200$). Stages in pollen development.

18. *Styphelia viridis*. 1-M. 19. *S. tubiflora*, 1-M. 20. *Astroloma humifusum*, mitosis in ovule tissue. 21-24. *A. pinifolium*. 21. Mitosis in leaf tissue. 22. 1-M. 23. 2-M. 24. 2-M, showing a residual first division bridge. 25-30. *Melichrus rotatus*. 25, 26. 1-M, showing typical chromosome arrangements. 27. 2-M, with a broken residual bridge. 28. 2-M. 29. Tapetal mitosis, 2 n. 30. Tapetal mitosis, 4n. 31. *Melichrus urceolatus*. 1-M.

Pollen development is unique, and in marked contrast to that of *Styphelia* and of *Astroloma humifusum*. The unbalanced chromosome number has apparently led to a breakdown of the "S" type of development. Following meiosis, the pollen mother cell is at first divided tetrahedrally, but the microspores vary in vitality in a way suggestive of the segregation of lethals or of small chromosome segment deficiencies. Rarely all four microspores may develop, giving a tetrad of pollen grains which are, however, only loosely held together. More often one, two, three, or even all the microspores in a tetrad may fail to develop, giving groups of single, paired and triplet pollen grains, in which the aborted cells can still be distinguished (Plate iv, fig. 32). In Table 4 is presented data on the numbers of microspores per tetrad developing fully, for 6 plants from the Audley locality, but similar behaviour was found in plants from La Perouse and Hornsby. Not only does the cause of this pollen failure require detailed investigation, but the condition might provide a favourable circumstance for a study of the occurrence of preferential segregation, as pointed out by Catcheside (1944) or of the effect of haploid lethals or deficiencies, since all the products of each meiosis may be recovered together.

TABLE 4.
Pollen Fertility per Tetrad in Astroloma pinifolium.

Plant No.	Number of Good Pollen Grains per Tetrad.					Total.	% Fertility.
	0	1	2	3	4		
1	78	229	170	35	2	514	33.1
2	118	58	19	5	0	200	13.9
3	66	90	39	5	0	200	25.4
4	148	165	70	17	0	400	21.2
5	97	182	106	16	5	406	28.4
6	148	137	102	13	0	400	23.8
Total ..	655	861	506	91	7	2120	25.63

3. *Melichrus* R. Br. A genus of only two species, both eastern in occurrence. At 1-M, both species have a haploid number of 8 (Text-figs. 25, 26, 31; Plate iii, fig. 6), and this number has been checked at 2-M (Text-fig. 28; Plate iii, fig. 7). In both species meiosis appears to be regular, and pollen development is of the "S" type.

Although both species are tetraploid with respect to the haploid complement of *Styphelia*, secondary association is not very evident. In the absence of this attraction, the chromosomes tend to assume a stable arrangement, as demonstrated by Kuwada (1929) and Ogawa (1929). Table 5, however, shows that there is a tendency for the arrangement of a ring of 6, with 2 centrally placed, to predominate in the present material.

TABLE 5.
Chromosome Arrangement in Melichrus rotatus.

Type of arrangement	8 (0)	7 (1)	6 (2)	5 (3)	Total.
No. of observations 1-M	1	7	15	1	24

Occasional bridges in both species indicate that the plants are heterozygous for small inversions. Text-fig. 27 illustrates a residual first division bridge at 2-M. The section of the chromosome between the two centromeres has been stretched to breaking point, and the centromeres have been prevented from complete entry into the two metaphase plates.

In *M. rotatus* excellent crush preparations were obtained showing tapetal mitoses. In anthers at a stage just younger than the commencement of meiotic prophase, abundant tapetal mitoses are sometimes found. The cells may be diploid (Text-fig. 29; Plate iii,

fig. 8), tetraploid (Text-fig. 30; Plate iii, fig. 9) or even octoploid, in the same anther. A similar condition in tapetal cells has been described by Cooper (1933) and many others in the angiosperms, and is apparently typical of tapetal tissue. Such divisions may be unsafe for the determination of the degree of ploidy in a plant, but since the chromosomes are much contracted, and can frequently be obtained well separated, they have a confirmatory value for checking determinations made from meiotic stages, or from ovule or leaf crushes.

4. *Trochocarpa* R. Br. This genus, like all those previously dealt with, is limited to Australia. It contains about seven species, but only one of these extends into New South Wales, and one species is western.

Trochocarpa laurina was examined from National Park, where it is not abundant. It is one of the very few members of the family which attain tree size. The haploid chromosome number, determined at 1-M and 2-M of microsporogenesis, is ten (Text-figs. 32, 33), so that the species is a secondarily balanced polyploid with reference to the haploid set of four found in *Styphelia*. Chromosome behaviour during meiosis is essentially regular, but rarely bridges are found at 1-A and 2-A. Such irregularities occur in well under 1% of the pollen mother cells. In many cells at 1-M, one bivalent appears distinctly larger than the others, but at 2-M this size difference is not always detectable.

Pollen development is of the "T" type, as found in *Epacris*, and indicates that the method of pollen development is not uniform in all genera of the Styphelieae.

5. *Brachyloma* Sond. A genus of about seven species limited to Australia, and divided into two sections. Only *B. daphnoides* has been available, but this species has been studied from localities as far apart as the Lane Cove River, near Sydney, and Albury. The haploid chromosome number of the species is 9, as determined both at 1-M and 2-M (Text-figs. 35, 36; Plate iii, figs. 10, 11), and this number has been checked by counts of somatic mitosis in ovule tissue, where the diploid number of 18 was observed (Text-fig. 34). The species also shows occasional bridges, indicative that plants may be heterozygous for small inversions. Plate iii, fig. 12, shows a residual first division bridge at 2-A, connecting opposite poles of the two spindles.

An analysis of nucleolar numbers both at interphase (Text-fig. 37; Plate iii, fig. 13), and in early tetrad nuclei (Text-fig. 38) indicates that nuclei may frequently contain two nucleoli. Data on the frequency of multiple nucleoli is given in Table 6. Of the 212 actual nuclei represented in the data, 105, or 49.5%, possessed two nucleoli. These may be of more or less equal, or markedly different size, but a dark-staining heterochromatic body can usually be seen associated with each. Gates (1942) has discussed the significance of the number of nucleoli with reference to polyploidy or secondary polyploidy. A basic haploid chromosome set may be assumed to possess only one nucleolar organizing chromosome, and the occurrence of two such chromosomes may be accepted as evidence of either polyploidy, secondary polyploidy, or of the reduplication of chromosomes. The evidence consequently suggests that *Brachyloma daphnoides* is a secondary polyploid.

TABLE 6.
Nucleoli in PMC Nuclei, *Brachyloma daphnoides*.

No. of Nucleoli per PMC.	2	3	4	5	6	7	8	Total.
Interphase (2 nuclei)	15	11	16	—	—	—	—	42
Tetrad stage (4 nuclei)	—	—	5	8	8	6	5	32

Pollen development is of the "T" type, similar to that in *Trochocarpa laurina*. In both species, there may be a rare failure of microspores to develop, giving unbalanced tetrads of mature pollen, similar to those of *Astroloma pinifolium*. This occurrence demonstrates that the pollen development of *A. pinifolium* is essentially of the "tetrad" type, complicated by chromosomal or genetical unbalance.

6. *Lissanthe* R. Br. Closely related to *Brachyloma*, and connecting it, taxonomically, with *Leucopogon*, this genus contains only three species, all eastern. In the species examined, the haploid chromosome number is 7 (Text-figs. 39, 40, 41, 44; Plate iii, fig. 14), and the species are unbalanced in relation to the haploid set of *Styphelia*. In size, the chromosome bivalents approach those of *Styphelia* spp. and of *Leucopogon setiger*, and are distinctly larger than in either *Brachyloma* or *Trochocarpa*. Pollen development is of the "T" type. (Text-figs. 42, 43.)

7. *Leucopogon* R. Br. This is by far the largest genus of the Styphelieae, and one of the few which extends outside Australia, being represented by a few species in New Zealand, the Malay Archipelago, and the Pacific Islands. In Australia, the genus comprises about 130 species which have been divided into three sections and a large number of series. The second section is not represented amongst the species reported in this paper.

The genus shows considerable variation in chromosome numbers ($n = 4, 6, 10, 12, 24$) and differences in chromosome behaviour and method of pollen development.

Section i. *Perojoa*. Series a. *Psilostachya*.

L. amplexicaulis. This species, which has a straggling often prostrate habit, is restricted to the Port Jackson district. At diakinesis, 1-M and 2-M (Text-figs. 45, 46; Plate iii, fig. 15) the haploid chromosome number is 12. The chromosomes are of small size, about 1μ in length at 2-M, and may be crowded on the metaphase plate showing considerable secondary association. The meiotic divisions, however, appear quite regular, and the species must be regarded as allopolyploid in constitution. Pollen development is of the "S" type.

L. lanceolatus. A widespread species, which has been collected from localities as widely different in climate as the semi-rainforest gullies of the Pt. Jackson and Illawarra districts, and cold, dry slopes at elevations of over 4,000 ft. near Oberon. In the former situations it may have almost a tree-like habit, but in the latter it is a low, bushy shrub.

Counts have been made from both types of habitat, both at 1-M and 2-M. The haploid number is 24 (Text-fig. 47), and the chromosomes show considerable secondary association, but the crowded nature of the plates makes any analysis of such association almost impossible. The chromosomes are of small size, similar to those of the allied *L. amplexicaulis*, and meiosis appears quite regular. Pollen development is of the "S" type.

The wide range of ecological conditions inhabited by this species is of interest in relation to its highly polyploid condition. Manton (1937) has shown that in *Biscutella iaevigata* polyploid forms have a wider tolerance of ecological conditions than have diploid forms of the same species, and Stebbins (1940), Sax (1936) and Goodspeed and Bradley (1942) describe a similar ecological tolerance of polyploids in various groups of plants.

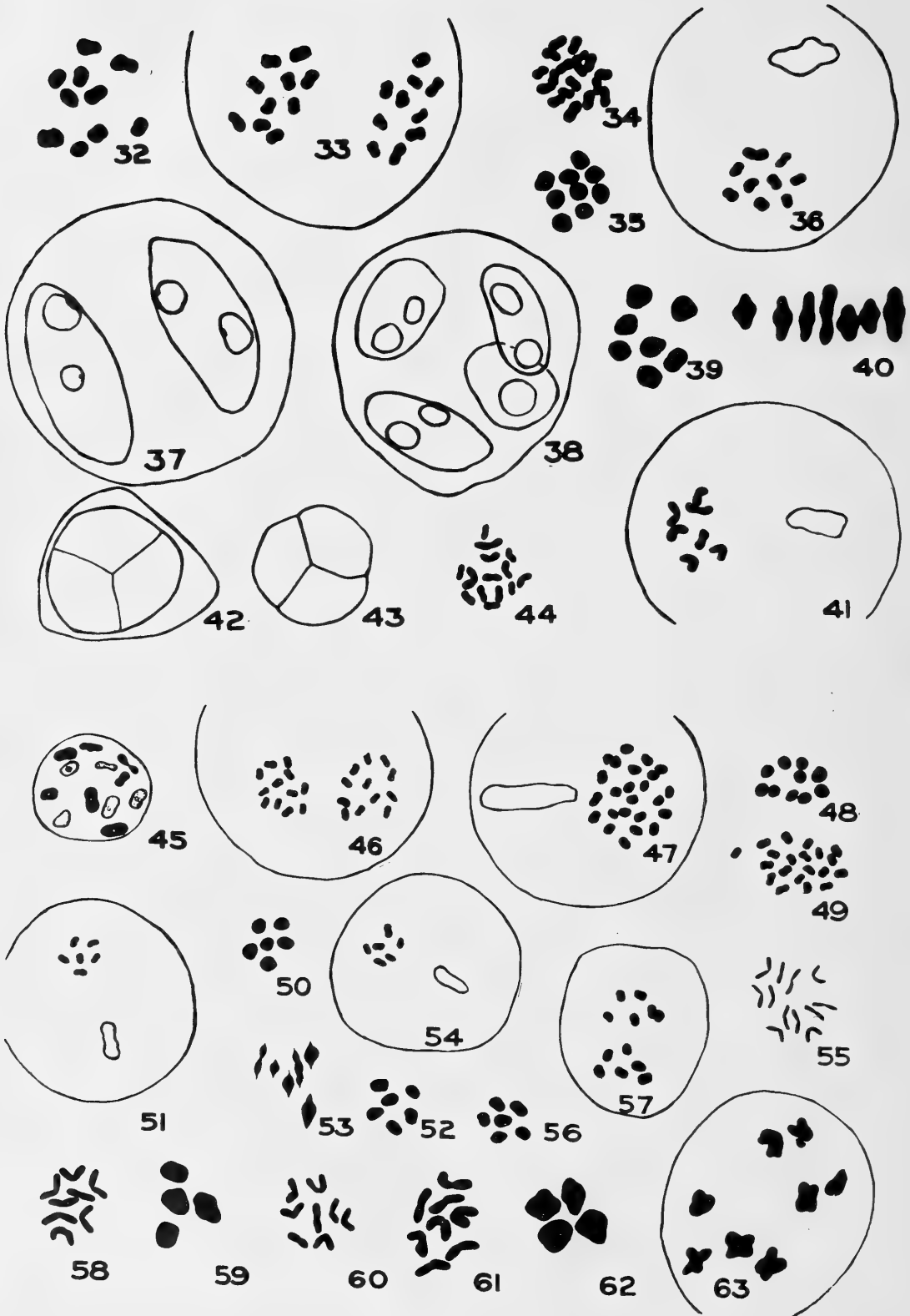
Series c. *Collinae*.

L. microphyllus. A species restricted to the Pt. Jackson-Blue Mountains districts, where it is extremely abundant. At 1-M and 2-M the haploid number is 6 (Text-figs. 50, 51; Plate iv, fig. 17) and meiosis is regular. The chromosomes are of small size, little more than 1 micron in length at second metaphase. Pollen development is of the "S" type.

Series g. *Virgatae*.

L. virgatus. In this species, which has a fairly extensive range, the haploid chromosome number of 10, found at 1-M and 2-M, has been checked by a count of 20 in several tapetal mitoses (Text-figs. 48, 49; Plate iii, fig. 16), in which the chromosomes were well spaced and easily countable. At 1-M secondary association is pronounced reaching a maximum of two groups of three bivalents and two secondary pairs, indicating a basic number of four. Meiosis appears quite regular, with a rare occurrence of chromosome bridges at 1-A and 2-A, and the species is probably amphidiploid in nature.

Pollen development is of the "T" type. The species is the only one within the genus, amongst those reported in the present paper, which does not show the "S" type



Text-figs. 32-63.

of pollen development. Two points are of interest in a comparison between *L. virgatus* and *L. microphyllus*, both placed in the same section of the genus. One has a haploid number of 6, shows little evidence of secondary association, and pollen development of the "S" type, but the other, with 10 bivalents, and showing marked secondary association also shows a loss of the "S" type of pollen development, and it is suggested that this loss may be associated with a change in genetic balance. The species is probably an amphidiploid between forms with haploid numbers of 4 and 6 chromosomes, and possibly involves hybridisation between different series or sections of the genus.

Section iii. *Pleuranthus*. Series b. *Ericoideae*.

L. ericoides. A widespread species occurring in all States except Western Australia. The haploid chromosome number of 6, determined at 1-M and 2-M (Text-figs. 56, 57; Plate iv, fig. 19), has been checked by a diploid count at somatic metaphase in ovule tissue (Text-fig. 55; Plate iv, fig. 18). The chromosomes are of smaller size than in *Styphelia* or in the 4-chromosome species of *Leucopogon*, and in ovule mitoses measure 1.8-2.0 μ in length, and are distinctly thinner, but they are otherwise uniform within the set. Pollen development is of the "S" type.

Series c. *Micranthae*.

L. esquamatus. A species practically confined to the Pt. Jackson district, where it is quite common. It possesses a diploid number of 8, determined in ovule mitoses (Text-fig. 58) where the chromosomes are of similar morphological appearance to those described for *Styphelia*, measuring 2.7-3.0 in length. At 1-M in the pollen mother cells, four bivalents of comparatively large size, are regularly formed (Text-fig. 59; Plate iv, fig. 20), and meiotic behaviour is normal. The bivalents are associated by chiasmata on both sides of the centromeres. Pollen development is of the "S" type.

Series d. *Planifoliae*.

L. setiger. A species restricted to the Pt. Jackson and Blue Mountains districts. The haploid counts of four obtained from 1-M, 1-A and 2-M stages (Text-figs. 62, 63; Plate iv, figs. 21, 22) have been confirmed from diploid counts on ovule tissue (Text-fig. 52) in which the chromosomes show the same features as in the previous species. Meiosis is quite regular, the bivalents at 1-M showing partially terminalized chiasmata, usually on both sides of the centromeres. The high apparent chiasma-frequency in this species is of special interest in relation to the cytological condition found in *L. juniperinus*. Pollen development is of the "S" type.

L. juniperinus. This species, which is confined to the Pt. Jackson district, except for isolated occurrences in Queensland and possibly in Victoria, has a somatic chromosome number of 12, determined from ovule crushes. The somatic chromosomes are of similar size and morphology to those of *L. setiger*, and are uniform within the set. In the meiotic divisions in pollen mother cells, behaviour is unusual, and of general cytological interest, and has been dealt with elsewhere (Smith-White, 1948). The species is apparently a true-breeding triploid hybrid between distantly related parents.

Series e. *Concavae*.

L. appressus. A species restricted to the Pt. Jackson district. The material examined is similar to specimens in the National Herbarium, and collected in the same locality.

The haploid chromosome number is 6, and the chromosomes are of similar size to

32, 33. *Trochocarpa laurina*. 32. 1-M. 33. 2-M. 34-38. *Brachyloma daphnoides*. 34. Mitotic chromosomes in ovule tissue. 35. 1-M. 36. 2-M. 37. Multiple nucleoli at interphase. 38. Multiple nucleoli at the tetrad stage. 39-43. *Lissanthe strigosa*. 39. 1-M. 40. 1-M, chromosomes in side view. 41. 2-M. 42, 43. Tetrads of young microspores ($\times 1,200$). 44. *Lissanthe sapida*. Mitosis in leaf tissue.

45 and 46. *Leucopogon amplexicaulis*, $n = 12$. 45. Diakinesis. 46. 2-M. 47. *Leucopogon lanceolatus*, $n = 24$. 2-M. 48 and 49. *L. virgatus*. 48. 1-M. 49. Tapetal mitosis, 2n. 50 and 51. *L. microphyllus*. $n = 6$. 50. 1-M. 51. 2-M. 52-54. *L. appressus*. 52. 1-M. 53. 1-M, side view. 54. 2-M. 55-57. *L. ericoides*. $n = 6$. 55. Mitosis in ovule tissue. 56. 1-M. 57. 2-M. 58 and 59. *L. esquamatus*. $n = 4$. 58. Mitosis in ovule tissue. 59. 1-M. 60-63. *L. setiger*. $n = 4$. 60. Mitosis in ovule tissue. 61. Mitosis in tapetal tissue. 62. 1-M. 63. 1-A. The repulsion of the chromosome arms is very apparent.

those of *L. ericoides* (Text-figs. 52, 53, 54), and show regular pairing. Pollen development conforms to the "S" type characteristic of the genus.

8. *Acrotriche* R. Br. A genus of about 10 species, limited to Australia. *A. serrulata* from Albury and *A. divaricata* from Springwood have been examined. In *A. divaricata* the somatic chromosome number is 18 (Text-fig. 64), as determined in leaf crushes. One pair of chromosomes in the somatic complement appear slightly longer than the remainder. In *A. serrulata*, at 1-M (Text-fig. 65; Plate iv, fig. 23) and at 2-M, the haploid chromosome complement is 9, and except for the occasional occurrence of chromosome bridges, chromosome pairing and behaviour is regular. Pollen formation, at least in the early stages, is of the "T" type, but mature pollen has not been available.

9. *Monotoca* R. Br. A genus of about eight species limited to Australia. The two species studied both show a haploid number of 12 at 1-M (Text-figs. 66, 67) which has been verified in tapetal mitoses (Plate iv, fig. 24). Regular bivalent formation, and pronounced secondary association is typical of both species. An analysis of secondary association is given in Table 7 for 34 pollen mother cells at 1-M of *M. elliptica*. Secondary pairs and triple groups are frequent, reaching a maximum of eight secondary associations if triple groups are counted as two secondary associations, following the method of Alam (1936), Raghaven (1938) and others, and the minimum number of separate groups observed is four in cell No. 27. The data support the view that the haploid chromosome set has been derived from a basic set of 4, but the occurrence of non-conformable associations, such as five or six pairs, suggests that the derivation has not been direct, but that it may have been derived from an initial rebalance, or secondary basic number of 6.

TABLE 7.
Secondary Association in Monotoca elliptica.

Cell No.	Singles.	Pairs.	Threes.	No. of Groups per Cell.	No. of Secondary Association.
1	1	1	3	5	7
2	—	6	—	6	6
3	3	3	1	7	5
4	2	2	2	6	6
5	—	3	2	5	7
6	3	3	1	7	5
7	3	3	1	7	5
8	1	1	3	5	7
9	—	3	2	5	7
10	2	2	2	6	6
11	3	3	1	7	5
12	—	3	2	5	7
13	3	3	1	7	5
14	1	4	1	6	6
15	1	1	3	5	7
16	1	4	1	6	6
17	2	2	2	6	6
18	2	5	—	7	5
19	—	3	2	5	7
20	2	5	—	7	5
21	1	4	1	6	6
22	2	2	2	6	6
23	2	2	2	6	6
24	4	4	—	8	4
25	1	1	3	5	7
26	2	2	2	6	6
27	—	—	4	4	8
28	1	4	1	6	6
29	1	1	3	5	7
30	1	1	3	5	7
31	1	1	3	5	7
32	—	3	2	5	7
33	3	3	1	7	5
34	5	2	1	8	4

Pollen development in both species is of the "S" type, although even in mature pollen the existence of the eliminated microspores may sometimes be fairly conspicuous.

B. TRIBE EPACRIDAE.

10. *Epacris* Cav. A genus of about 30 species in Australia, but it also extends to New Zealand. It is unrepresented in Western Australia. The type genus of the family, it is a natural and easily recognizable one.

In all seven species examined, the haploid chromosome number determined at 1-M and 2-M is 13 (Text-figs. 68, 69, 70, 71-75; Plate iv, figs. 25, 26), and chromosome pairing is regular, except for the rare occurrence of bridges and laggards. In *E. pulchella*, two separate bridges have been observed at 1-A in a single pollen mother cell (Text-fig. 73), and single bridges have a frequency of approximately 3-4% at this stage, indicating the presence within the species of small inversions. Secondary association reaches a maximum of three groups of 3, and one group of 4, suggesting that the basic number for the genus is four. Pollen development is regularly of the "T" type in all species.

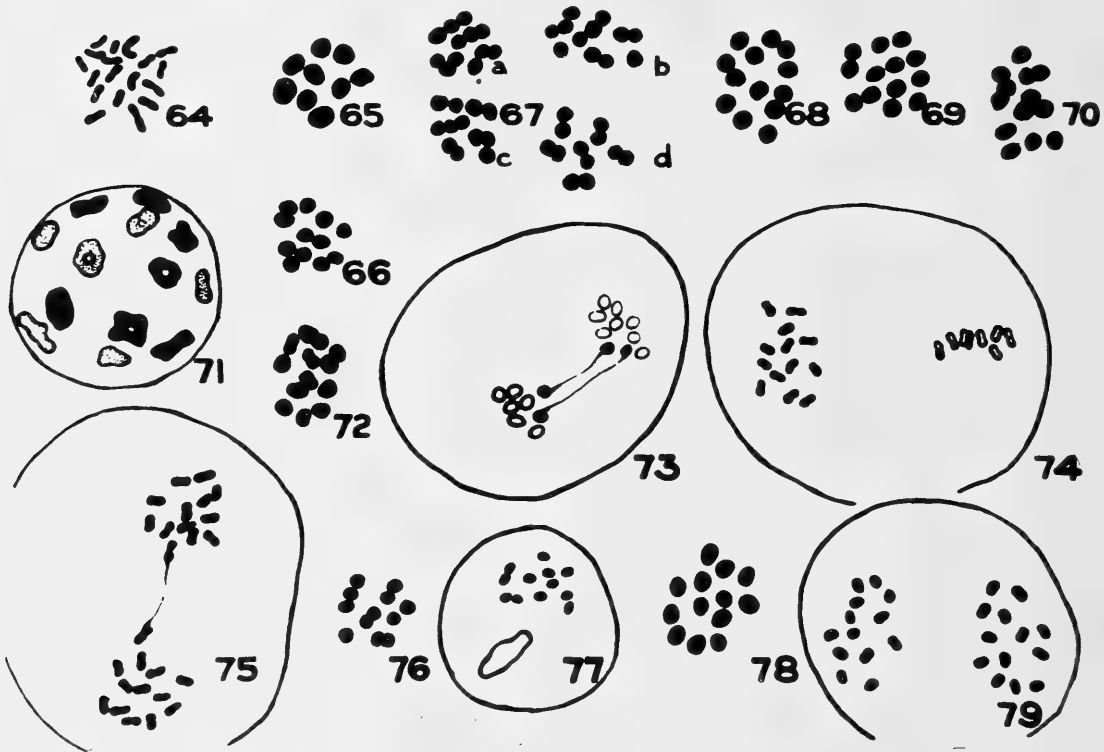
11. *Lysinema* R. Br. This genus is closely allied to *Epacris*, from which it differs mainly in the aestivation of the corolla. It contains 6-7 species but only one of these occurs in eastern Australia. *L. pungens* has been studied from localities at Gordon, Kuringai, Lane Cove River, and National Park. It is widespread and abundant around Sydney. The species shows a haploid chromosome number of 13, with regular chromosome pairing, and the chromosomes are of similar appearance to those of *Epacris*. Pollen development is again of the "T" type.

12. *Sprengelia* Sm. This genus contains three species, all of which are eastern. Only *S. incarnata* has been examined. Localities included were Kuringai and National Park. The species possesses a haploid number of 12 (Text-figs. 76, 77; Plate iv, fig. 27), and chromosome behaviour is quite regular. Secondary association is again pronounced (Table 8) and reaches a maximum of three groups of 3 at both 1-M and 2-M. Pollen development is of the "T" type.

TABLE 8.
Secondary Association in Sprengelia incarnata.

Cell No.	Singles.	Pairs.	Threes.	Fours.	No. of Groups per Cell.	Total Secondary Association.
1	2	2	2	—	6	6
2	4	4	—	—	8	4
3	1	4	1	—	6	6
4	2	2	2	—	6	6
5	2	2	2	—	6	6
6	1	4	1	—	6	6
7	4	4	—	—	8	4
8	3	3	1	—	7	5
9	4	1	2	—	7	5
10	2	5	—	—	7	5
11	1	4	1	—	6	6
12	3	1	1	1	6	6
13	7	1	1	—	9	3
14	5	2	1	—	8	4
15	6	3	—	—	9	3
16	2	5	—	—	7	5
17	1	4	1	—	6	6
18	4	4	—	—	8	4
19	—	1	2	1	4	8
20	2	2	2	—	6	6
21	1	4	1	—	6	6
22	3	—	3	—	6	6
23	3	3	1	—	7	5
24	2	5	—	—	7	5
25	2	5	—	—	7	5
26	1	4	1	—	6	6

13. *Dracophyllum* Labill. A genus of nine species (Bentham), but eight of these are confined to Western Australia. *Dracophyllum secundum* has been examined from localities at Lane Cove River and National Park. It possesses a haploid chromosome number of 13 (Text-figs. 78, 79; Plate iv, fig. 28), and chromosome behaviour is regular. Pollen development (Text is of the "T" type).



Text-figs. 64-79.

64. *Acrotriche divaricata*. Mitosis in leaf tissue. 65. *Acrotriche serrulata*. $n = 9$. 1-M. 66. *Monotoca scoparia*. 1-M. 67. *Monotoca elliptica*. Four 1-M plates illustrating degrees of secondary association. Figure 67a shows maximum association. 68. *Epacris longiflora*, $n = 13$. 1-M. 69. *Ep. paludosa*. 1-M. 70. *Ep. microphylla*. 1-M. 71-75. *Ep. pulchella*. 71. Diakenesis. 72. 1-M. 73. 1-M, showing two bridges. 74. 2-M. 75. 2-M, with a residual 1st division bridge. 76 and 77. *Sprengelia incarnata*. 76. 1-M. 77. 2-M. 78 and 79. *Dracophyllum secundum*. 78. 1-M. 79. 2-M.

4. GENERAL DISCUSSION.

THE BASIC CHROMOSOME NUMBER OF THE ERICALEA.

It is to be expected that the demonstration of a "basic" number for an Order, or other large systematic category, can be at best indirect and circumstantial, since those changes of greatest phylogenetic significance are likely to be of remote origin, and the characteristic features of polyploidy will have been lost in the subsequent evolution of the groups. Wanscher (1934b) has suggested that many families and higher categories have low basic numbers, and in a few cases this has been well established (e.g., in the Pomoideae, Darlington and Moffett 1930, Moffett 1931).

Evidence for the existence of a "basic" number in large groups, however, may be of several kinds. The existence in any genera of low numbers which are factors of the dominant higher numbers in the whole group, is always suggestive since there are severe barriers to any considerable reduction in number. In addition, data on secondary association, on the occurrence of multiple nucleoli, on chromosome morphology, on the

occurrence of autopolyploidy, inheritance in haploids or triploids, and complex genetic inheritance may be available (Darlington, 1937, p. 240).

In the Ericales, Hagerup (1928) suggested that 6 would be the basic number, on the evidence of secondary association and of the actual occurrence of that number in the Diapensiaceae and in *Phyllodoce* (cf., however, Wanscher, 1934a). On a re-examination of the data of secondary association in the Ericaceae, and on the existence of a haploid number of 8 in *Calluna*, Wanscher (1934a) suggested that the basic number for the Order is 4.

Table 9 gives a summary of the records of chromosome numbers for the Ericales, which has been prepared from the lists of Tischler (1927, 1931, 1936, 1937, 1938) and Gaiser (1926, 1930a, 1930b, 1933), and from Darlington and Janaki (1944).

In the Epacridaceae, chromosome numbers are exceptionally variable, but the actual existence of a haploid number of 4 in *Styphelia* and *Leucopogon* is strong evidence in support of Wanscher's view, although reduction in chromosome number from 6 to 4 could result from segmental interchange followed by the loss of centromeres, as demonstrated by Tobgy (1943) in *Crepis*.

The evidence from secondary association presented for *Monotoca* and *Sprengelia*, both with a haploid number of 12, also supports the view that the primary basic number is 4. In these genera, secondary association is very marked and reaches a maximum with four groups of three, but non-conformable arrangements, such as six pairs, suggest that the present set has been derived indirectly, by polyploidy following the establishment of a secondary basic number of six. Data on chromosome size also support this view (v. infra). Thus the views of both Hagerup and Wanscher receive some confirmation.

The occurrence of multiple nucleoli at both interphase and in microspore nuclei in *Brachyotoma daphnoides* ($n = 9$), provides additional evidence that the chromosome number in that species is a derived one, either by polyploidy or by reduplication of a nucleolar chromosome.

TABLE 9.
Summary of Chromosome Numbers in the Ericales.

	Number of Genera and Species with Basic Gametic Chromosome Numbers (including Polyplods).							
	6	8	9	11	12	13	19	23
Clethraceae ..		1/1						
Ericaceae (including Vaccinaceae) ..	1/1	1/1	1/1	2/14 1/1	15/42	5/47	1/1	1/1 1/3
Pyrolaceae ..								
Epacridaceae ..						1/1		
Diapensiaceae ..	5/5							

THE PHYLOGENY AND TAXONOMY OF THE EPACRIDACEAE.

Cytological data on the Epacridaceae lead to several inferences dealing with its phylogenetic relationship with the Ericaceae and other families of the Ericales, and these are at variance with inferences drawn from morphology. Which of the two lines of evidence should be given greater weight, must perhaps remain for the time being a matter of opinion. Turrill (1942) does not consider cytological data any more "ultimate" with regard to phylogeny than data drawn from morphology, physiology or ecology, but believes cytology may be of special value above the species level.

The Epacridaceae has generally been considered a derived group (e.g., Rendle, 1938), owing to certain highly specialized characters, especially of floral morphology, which it exhibits. It shows a development of gamopetally, of epipetally, reduction in the numbers of stamens, and an unusual method of anther dehiscence, in which both anther locules open by a common slit. Throughout the angiosperms, gamopetally and epipetally are considered to be derived from a primitive condition with free petals and hypogynous

stamens (e.g., Hutchinson, 1926). The reduced number of stamens, as compared with the Ericaceae, is also considered a phylogenetically advanced character, and in the Diapensiaceae, which has the same reduced number, a second whorl of stamens is sometimes represented by staminodes. Turrill (1942) has set out amongst general principles applying to the deduction of phylogeny, that specialization is to be considered as derived, unless there is evidence of reduction, and that in a graded series, phylogeny should be read from the type closest to the form accepted as lower in the evolutionary scale. On these criteria the Epacridaceae must be considered as a highly specialized group of the Ericales, and its general resemblance to the tribe Ericoideae of the Ericaceae would suggest its derivation from that group.

Within the Epacridaceae, the Epacrideae show the closest resemblance to the Ericaceae, and on the same reasoning might be considered as primitive to the Styphelieae. The peculiar method of pollen development described for some genera of the latter group supports this inference. Such an abnormal method, not found elsewhere in the angiosperms, is obviously derived from the tetrad type of development usual in the Ericales. Moreover, the Epacrideae is connected with the Ericoideae by the "transition" genera, *Prionotes* and *Lebetanthus*.

The cytological evidence presented in this paper indicates, however, that the basic number for the Epacridaceae and even for the whole of the Ericales, is four, and consequently genera such as *Styphelia* and *Leucopogon* could not be derived from any type of the Epacrideae or Ericoideae, in both of which the chromosome number is 12 or 13. In order to fit these two opposing sets of evidence, it becomes necessary to assume that there have been several independent lines of evolution from primitive ancestral Ericales stock, which possessed a haploid chromosome number of 4, free petals and stamens, separate dehiscence of the anther locules, and tetrad pollen. The tribe Epacrideae might be in fact actually derived from the Ericoideae, since the geographical distribution of the two groups overlaps in Tasmania. The Styphelieae, however, must be given a separate origin, and the Epacridaceae is to be considered a polyphyletic family.

With regard to the taxonomy of the Styphelieae, the wide variation in chromosome number in that group provides justification for the maintenance of the genera established by R. Brown, and possibly for a further subdivision of genera such as *Leucopogon* and *Astroloma*.

EVOLUTIONARY PROCESSES AND SPECIATION IN THE EPACRIDACEAE.

Babcock (1934, 1942) has dealt with the nature of the internal processes leading to speciation, and has shown that the main primary processes are gene mutation, structural chromosome alteration, and alteration in chromosome number, including polyploidy, whilst hybridization is a secondary but very important process.

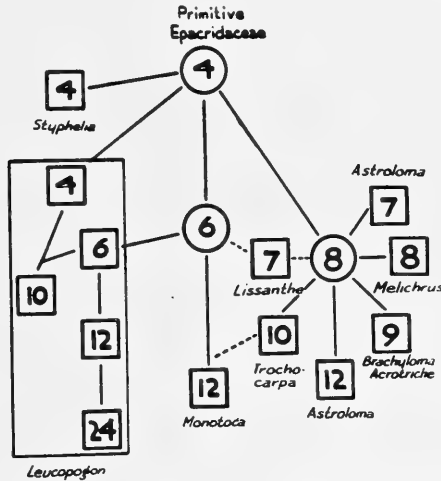
Alteration in chromosome number. Depending on the circumstances of speciation, the chromosome numbers of any group may show great variability, as, for example, in the genus *Carex* (Heilborn, 1924) and *Scirpus* (Hicks, 1928), or may be constant, or almost constant, as in *Antirrhinum* ($n = 8$, Baur, 1932), *Rhododendron* ($n = 13$, Sax, 1930), the Pomoideae ($n = 17$, Moffett, 1931), the Myrtaceae ($n = 11$, Atchison, 1947), and the Gymnosperms (Sax and Sax, 1933). Depending on these circumstances, differences in chromosome number may have either considerable or little taxonomic value and phylogenetic significance. Smith (1933) has shown that in *Primula*, differences in chromosome number have some value as sectional criteria, but are probably of less significance phylogenetically in that group than differences in chromosome size.

Alteration in chromosome number has played a considerable part in the development of the Epacridaceae. Assuming the primitive number to be four, the following trends are evident:

- (a) Simple tetraploidy, giving a haploid number of 8 (*Melichrus*).
- (b) Following tetraploidy, there has been a gain (*Brachyloma*, *Acrotriche*) or loss (*Lissanthe*, *Astroloma pinifolium*) of a centromere, probably resulting from translocations or other structural changes. Gain or loss of genic material, which is not necessarily involved, causes less unbalance in polyploids than in diploids.

- (c) The attainment of a secondarily-balanced number of 6 (*Leucopogon* spp.). How this number may have originated cannot be suggested, but it is possibly one of the most important steps in the evolution of the group.
- (d) The development of the 12 chromosome set (*Leucopogon* sp., *Monotoca*, *Sprengelia*) either directly by hexaploidy from the basic set of 4, or more probably by tetraploidy on the secondary basic set of 6.
- (e) The establishment of further secondary balance with a chromosome number of 13 (*Epacris*, *Lysinema*, *Dracophyllum*).
- (f) The co-existence of chromosome numbers of 4 and 6 in the same genus has made possible the origin by hybridization of amphidiploids. *Leucopogon virgatus* may be of such origin.

These chromosome relationships are represented graphically in the following diagram (Text-fig. 80), which, however, is not claimed to represent any phylogenetic significance.



Text-fig. 80.—Chromosome Number Relationships in the Styphelieae.

Structural Chromosome Change. The occurrence of bridges at first and second anaphase in practically all plants of all species examined indicates that the species are heterozygous for small inversions, and it is reasonable to assume that other structural changes, less easily detectable, may also have occurred. That the inversions are of small size is suggested by the fact that they are nowhere abundant. They may, however, have considerable significance in relation to alterations in chromosome number. Tobgy (1944) has demonstrated that crossing over between structurally dissimilar chromosomes in *Crepis* may lead to the transference of nearly all the genic material from one chromosome to another, leaving an almost naked centromere, which may easily be lost at subsequent divisions.

Changes in Chromosome size. There is an apparent correlation between chromosome number and chromosome size in the Styphelieae, those species with the smallest number having the largest chromosomes (*Styphelia*, *Leucopogon* spp.). This does not mean that the larger numbers have been derived by fragmentation. The necessity that each fragment must contain a centromere if it is to function at each nuclear division renders any such assumption untenable. It is known that genotype exerts a considerable influence on chromosome size, and it may be assumed that in any group there is both an optimum cell-size and optimum size relationship between the cell, the nucleus and the chromosomes. Following increase in chromosome number, natural selection would then lead to a gradual reduction in chromosome size, until the optimum relationships become re-established.

The most marked discontinuity in chromosome size is between the 4-chromosome and 6-chromosome species of *Leucopogon* (cf. Plate iv, figs. 17, 19, 20, 21). The smaller

size of the chromosomes in *L. ericoides*, for example, is not balanced by the increase in number, and the total volume of the chromosomes is much less than in the 4-chromosome species.

In some groups of plants, differences in chromosome size have been shown to have considerable phylogenetic significance (Smith, 1933) and since the chromosomes of *Leucopogon amplexicaulis* ($n = 12$), *L. lanceolatus* ($n = 24$), and *Monotoca* ($n = 12$), compare in size with those of *L. ericoides*, *L. appressus* and *L. microphyllus* ($n = 6$), rather than with those of *L. setiger*, *L. esquamatus* and *Styphelia* spp. ($n = 4$), it is suggested that the higher haploid numbers have been derived from a secondary basic number of 6, similar to that of *L. ericoides*, rather than by direct hexaploidy from a basic set of 4. Although the evidence of chromosome size needs more careful and detailed study, it supports the conclusions drawn from the phenomena of secondary association.

POLLEN DEVELOPMENT AND CHROMOSOME BALANCE IN THE STYPHELIEAE.

The unusual "S" type of pollen development, found in most genera of the tribe Styphelieae, is probably genetically or genotypically controlled. It must involve the presence of polarity, or of a gradient, in the pollen mother cell similar to that found in the linear tetrad of megaspores, only one of which normally develops into an embryo sac, or to that of the animal oocyte, which throws off three polar bodies at meiosis. That this polarity is intracellular, rather than in the form of a gradient extending over the whole anther, is shown by the random arrangement of the pollen grains in the anther, as seen in longitudinal section.

The existence of this intra-cellular polarity has modified the normal tetrad type of development generally characteristic of the Ericales, and causes an abnormal regularity in the behaviour of univalents in *Leucopogon juniperinus* (Smith-White, 1948). Here it is desired to emphasize the relationship which evidently exists between chromosome number and method of pollen development. An examination of Table 1 shows that all those species of the Styphelieae possessing a haploid number of 4 or 6, or multiples of these numbers, exhibit the "S" type of pollen development, whereas the species with aneuploid numbers ($n = 7, 9, 10$) have tetrad pollen. This correlation is maintained even within a genus. In *Leucopogon*, eight species with 4, 6, 12 or 24 chromosomes possess the "S" type of development, whilst one, *L. virgatus*, with 10 chromosomes, has tetrad pollen. A similar condition exists between *Astroloma humifusum* ($n = 12$) and *A. pinifolium* ($n = 7$).

Whilst the "S" type of pollen must be regarded as a specialization from the tetrad type, the examples of tetrad pollen in the Styphelieae are most logically accounted for by a breakdown of the delicate mechanism controlling the intra-cellular polarity, with a consequent reversion to the more primitive condition. They do not, therefore, deny a close relationship between the various genera of the tribe.

SUMMARY.

Chromosome numbers are reported for 13 genera and 36 species of the Epacridaceae. Chromosome numbers are variable and include haploid numbers of 4, 6, 7, 8, 9, 10, 12, 13 and 24.

On the basis of chromosome number relationships, on secondary association, the occurrence of multiple nucleoli, and chromosome size relationships, the basic number for the family is considered to be 4. Alterations in chromosome numbers have involved the establishment of a secondary basic set of 6, polyploidy, gain and loss, and in one case, probably amphidiploidy.

The existence of structural changes, as evidenced by the occurrence of bridges at 1-A and 2-A, is considered to provide the opportunity for aneuploid change in chromosome number.

The phylogeny of the Epacridaceae has been discussed on the basis of data from morphology, geographical distribution and cytology. The cytological and morphological data can be made conformable by the assumption that the Styphelieae and Epacrideae

have had separate origins from basic Ericales stock, and that the Styphelieae is not derived from the Ericoideae. On this reasoning, the Epacridaceae would be polyphyletic.

An unusual polarized type of pollen development is described for *Styphelia* and related genera. This type is obviously derived from the tetrad type of pollen development characteristic of the Ericales. It is apparently genetically controlled, and is liable to breakdown, with reversion to tetrad pollen, following genetic or cytological unbalance.

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EXPLANATION OF PLATES.

PLATE III.

All photographs are at a magnification of $\times 2,000$.

Figs. 1-3, *Styphelia longifolia*. 1. Mitotic metaphase in ovule tissue. 2. 1-M. 3. 2-M. Figs. 4 and 5, *Astroloma pinifolium*. 4. 1-M. 5. Persistent 1st division bridge at 2-M. Figs. 6-9, *Melichrus rotatus*. 6. 1-M. 7. 2-M. 8. Diploid metaphase in tapetal tissue. 9. Tetraploid metaphase in tapetal tissue. Figs. 10-13, *Brachyloma daphnoides*. 10. 1-M. 11. 2-M. 12. Persistent 1st division bridge at 2-A. 13. Interphase, with two nucleoli in both nuclei. Figs. 14-16: 14. *Lissanthe strigosa* 1-M. 15. *Leucopogon amplexicaulis* 2-M. 16. *Leucopogon virgatus* metaphase in tapetal tissue.

PLATE IV.

Photographs are at $\times 2,000$, except figures 30-32.

Fig. 17. *Leucopogon microphyllus* 1-M. 18 and 19. *Leucopogon ericoides*. 18. Mitotic metaphase in ovule tissue. 19. 1-M. 20. *Leucopogon esquamatus* 1-M. 21 and 22. *Leucopogon setiger*. 21. 1-M. 22. 1-A. 23. *Acrotriche serrulata* 1-M. 24. *Monotoca elliptica*, mitosis in tapetal tissue. 25. *Epacris paludosa* 1-M. 26. *Epacris microphylla* 2-M. 27. *Sprengelia incarnata* 1-M. 28. *Dracophyllum secundum* 1-M. 29. *Styphelia triflora*. A pollen mother cell with four microspore nuclei showing the polarized rearrangement of the nuclei. 30 and 31 ($\times 900$). *Styphelia triflora*. 30. A later stage than fig. 29, showing the formation of unequal microspores. 31. A young pollen grain. Only one microspore develops. 32 ($\times 240$). *Astroloma pinifolium*. Mature pollen.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART V.* THE PALPOMYIA GROUP OF GENERA.

By DAVID J. LEE, B.Sc.

(With Plate v and 20 Text-figures.)

[Read 28th April, 1948.]

INTRODUCTION.

Some 22 generic names have, at one time or another, been used for species included in this group. Of these, twelve are recognized as valuable by Macfie (1940), the rest being relegated to synonymy. Of the available genera I have recognized species belonging to only six in the material available to me for study. These are *Palpomyia*, *Clinohoelea*, *Xenohoelea*, *Johannsenomyia*, *Dicrohoelea*, and *Heteromyia*. As far as I have been able to check, the species which I have assigned to each of these genera conform fairly closely to their respective genotypes and all species run to the genus within which they have been included in Macfie's key, with the exception of those included in *Heteromyia*. Nevertheless the generic circumscriptions cannot yet be considered stable and changes may eventually be necessary.

In the following pages will be found a fairly detailed description of the characters of the genus *Palpomyia* and brief statements of the way in which the other genera may be differentiated from *Palpomyia*. It will be seen that the differences are rather more arbitrary than is desirable in generic segregations, but until a detailed study of a group, correlated with regional distributions, has been undertaken, it will remain impossible to do more than separate species in the most convenient way possible, without regard to natural affinities. Hence it should be realised that when genera are defined by their outstanding points of difference from another better known genus, it does not necessarily mean that they agree in all points not specifically mentioned, but only that they are otherwise similar in most respects.

The *Palpomyia* group comprises some of the largest species of Ceratopogonidae, and are all apparently predatory forms.

Genus PALPOMYIA Megerle.

MEGERLE VON NUEHLESELD, J. G., in MEIGEN, J. W., 1818.—"Systematische bekannten europäischen zweiflügeligen Insecten", 1: 35 and 65 (not seen).

GOETGHEBUER, M., 1920.—*Mem. Mus. Hist. Nat. Belg.*, 8, fasc. 3: 77.

EDWARDS, F. W., 1926.—*Trans. ent. Soc. Lond.*, 1926: 416.

Synonymy: *Apogon* Rondani, C., 1856. "Dipterologiae Italicae prodromus", 1 (not seen, fide Macfie, 1940). *Alasion* Rondani, C., 1857. "Dipterologiae Italicae prodromus", 2 (not seen, fide Macfie, 1940). *Heteromyia* Say of Kieffer 1926 in part but not *Heteromyia* Say of Macfie 1940.

GENERIC CHARACTERS.

The genus *Palpomyia* comprises species of usually moderate to large size with slender, almost bare bodies. The eyes are bare and separated, the palpi slender and the third segment not enlarged. The female antennae have segments 3-10 oval with sparse verticils, and 11-15 cylindrical and considerably elongated. The plumes of the male antennae are sometimes inconspicuous. In many species the scutum bears a small tubercle or spine at the middle of the anterior border and the surface is clothed

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with fine hairs only. The lateral piece of the scutum is broad, the posterior pronotal plate large and including the prothoracic spiracle and the pleura are almost entirely chitinized, the anepisternal cleft being narrow and oblique. The femora of the fore-legs are more or less thickened and with at least a few spines on the undersurface, those of the posterior legs are slender, sometimes with a few fine spines. The fourth tarsal segment is cordiform or bilobed beneath but unarmed, the fifth may be bare or with a few slender, curved, pointed spines and the claws are equal, of moderate size and with or without a small tooth on the inner side near the base. The wings are relatively long and narrow, with fine microtrichia but without macrotrichia. The costa extends to at least two-thirds of the wing length, both radial cells are well formed, the second being much longer than the first. There is no intercalary fork, the media is broadly sessile and r-m is vertical or nearly so. In many species the female abdomen has a pair of eversible glands between segments VII and VIII and usually similar pairs of glands between some of the other segments as well. When these glands are present the corresponding tergites have pairs of long, spinelike internal projections from their anterior margins (seen only in cleared specimens). The male hypopygium is partially or completely inverted. The ninth tergite is rather small, the cerci are well developed and the harpes are usually fused into a single median structure with rounded tip but may occasionally be divided distally.

Records of the Genus Palpomyia in the Australasian Region.

Although Kieffer described two species in the genus *Palpomyia*, these have been put by me into other genera. One, *bifasciata*, is now in *Clinohoelea*, and the other, *imparunguis*, was renamed *australiensis* by Kieffer, and placed in genus *Mixohoelea*, which is here regarded as a synonym of *Xenohoelea*. Strictly, then, the genus has not previously been recorded from Australia or New Guinea, although a number of species correctly assigned to *Palpomyia* have been described from New Zealand.

Apart from the two species described as new below, one from Tasmania, the other from Canberra, there are also included in the material lodged in the C.S.I.R. Museum a few specimens which proved inadequate for description but which extend the known range of the genus in the region. A series from Tullamore, New South Wales (ix:1946, D. H. Colless), come close to *P. subalpina*, but are rather too shrivelled for exact determination, and a single specimen of what is almost certainly a new species comes from Sogeri, Papua (31:v:1947, D. J. Lee).

Key to Australasian Species of Palpomyia.

1. Legs with dark markings on apices of femora and tibiae. (Fore femora much swollen with 15-18 spines; gland rods of female abdomen poorly developed but present on tergites VI and VII) *urpicifemoris* I. & M.
Femora and tibiae otherwise marked 2
2. Fore femora with dark band at middle (fore femora swollen with 15-20 spines; gland rods well developed at least on tergites V-VII) *cantawris* Macfie
Fore femora not darkest at middle 3
3. No anterior tubercle (fore femora only slightly swollen with 10 spines; gland rods absent) *decima* n. sp.
Anterior tubercle present 4
4. Legs almost uniformly yellowish brown. (Fore femora a little swollen with 10 spines; gland rods present on tergites III-VII) *rastellifer* Macfie
Legs darker brown, particularly hind tibiae 5
5. Fore tibiae lighter than those of the four posterior legs. (Fore femora a little swollen with about 13 spines in the female; gland rods present on tergites V-VII.) *nelsoni* Macfie
Fore tibiae dark brown. (Fore femora swollen with about 15 spines; gland rods absent.) *subalpina* n. sp.

PALPOMYIA DECIMA, n. sp.

Types: Holotype ♀, allotype ♂ and three female paratypes in the C.S.I.R. Museum.

Type Locality: Geeveston, Tasmania (7:xii:1922, A. Tonnoir for holotype, 6:xii:1922 for allotype and two paratypes, 8:xii:1922 for the third paratype).

DISTINCTIVE CHARACTERS.

The absence of any gland rods in the female abdomen distinguishes this species from any which have previously been described and legitimately belong in this genus

(only those described from New Zealand by Ingram and Macfie, 1931 and Macfie 1932). Other characters differentiating it from *P. subalpina* are detailed under that species.

DESCRIPTION.

(See Table 1 for measurements.)

Female.

Head: The head is very dark brown, almost black, with the eyes rather widely separated. The antennae are dark brown with segments 4-10 ovate and the last five elongated. The mouthparts are short, less than half the height of the head.

Thorax: This is almost black with brown pubescent hairs on scutum and scutellum, the latter with three border bristles on each side. There is no anterior tubercle and the halteres are dark brown.

Legs: These are as dark as the body but with the tarsi slightly lighter and reddish. The fore femora (Text-fig. 1) are only slightly swollen with a group of ten spines beneath on the distal half. The fourth tarsal segments are cordate and the claws are small, equal and with a basal angle (Text-fig. 2).

Wings: Macrotrichia are absent but fine microtrichia are present over the wing surface, just visible at a magnification of 60 \times . The area of membrane encompassed by the costa, the base of M to r-m and R₄₊₅ is brownish. The venation is shown in the photograph in Plate v, fig. 1. The two lower (posterior) sides of the first radial cell are distinctly unequal and the cell thus approaches a parallelogram in shape.

Abdomen: This is dark brown. No gland rods are present and there are two subequal spermathecae.

Male.

This sex is generally somewhat lighter in colour. The antennae are lighter brown with long dark brown verticils on segments 2-9. The legs are light brown and the fore femora are slightly swollen and spinose beneath on the distal half.

Genitalia (see Text-fig. 3): The coxites are simple with the style rather short and tapering. The phallosome is a simple inverted V-shaped organ and the harpes are paired, elongated clubs. The ninth sternite is large and broad, bluntly rounded apically and covering as a definite chitinous flap the greater part of the rest of the terminalia.

Distribution: Apart from the type series I have examined, a further specimen from Eaglehawk Neck, Tasmania (6:xi:1922, A. Tonnoir).

PALPOMYIA SUBALPINA, n. sp.

Types: Holotype ♀ and two female paratypes in the C.S.I.R. Museum.

Type Locality: Blundell's, Australian Capital Territory (7:i:1930, A. Tonnoir).

DISTINCTIVE CHARACTERS.

This species is very similar to *P. decima* but is slightly larger, with the fore femora a little more swollen and with more spinules. A minute anterior tubercle is present and the first radial cell of the wing is distinctly triangular.

DESCRIPTION.

(See Table 1 for measurements.)

Female.

Head: This is black and shining with the eyes rather widely separated. The pedicels of the antennae are black and the flagellum dark brown; the basal flagellar segments (4-9) are about twice as long as broad and segment 3 is twice the length of 4; segment 10 is a little longer than the preceding flagellar segments and 11-15 are considerably elongated. The clypeus is black and prominent and the mouthparts are scarcely half the height of the head.

Thorax: The thorax is entirely black and shining with scutum and scutellum clothed with pubescent hairs. A minute anterior tubercle is present and the halteres are very dark with black knobs.

Legs: The mid and hind femora and tibiae, the fore tibiae and the third to fifth tarsal segments of all legs are dark brown, the rest of the legs being a lighter, yellowish

brown. The fore femora are distinctly, but not excessively swollen with about fifteen spines on the undersurface (Text-fig. 4). The fore tibiae are curved at the base only. The third tarsal segments are short, the fourth cordate, the fifth longer and with the claws short, equal and each with a basal angle.

TABLE 1.
Various Measurements of Species of *Palpomyia*.

Legs.	<i>Palpomyia decima</i> .			<i>Palpomyia subalpina</i> .	
	Wing Length (holotype ♀) 2.76 mm.			Wing Length (paratype ♀) 2.96 mm.	
	Fore Leg (Paratype ♀).	Hind Leg (Paratype ♀).	Hind Leg (Allotype ♂).	Fore Leg (Paratype ♀).	Hind Leg (Paratype ♀).
Femur	0.714 mm.	1.020 mm.	0.850 mm.	0.822 mm.	1.222 mm.
Tibia	0.680 "	0.986 "	0.765 "	0.780 "	1.092 "
Tarsus I	0.323 "	0.544 "	0.408 "	0.416 "	0.650 "
" II	0.153 "	0.238 "	0.204 "	0.156 "	0.286 "
" III	0.085 "	0.119 "	0.102 "	0.091 "	0.130 "
" IV	0.076 "	0.085 "	0.068 "	0.078 "	0.078 "
" V	—	0.136 "	0.119 "	0.130 "	0.156 "
Claw	—	0.051 "	0.051 "	0.052 "	0.065 "

Wings: The venation is very similar to that of *P. decima* but the first radial cell is distinctly triangular, due to the two lower (posterior) sides being subequal. The anterior part of the wing membrane bounded by the costa, the base of the media and R_{4+5} is brownish.

Abdomen: This is very dark brown, almost black, shining, with no apparent gland rods.

The male is not known.

Distribution: Only known from the type locality.

PALPOMYIA CANTUARIS Ingram and Macfie.

INGRAM, A., and MACFIE, J. W. S., 1931.—*Ann. Trop. Med. and Parasit.*, 25: 207.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26: 50.

Type: Type female in British Museum (Natural History).

Type Locality: The first listed locality is South Canterbury, New Zealand.

Distribution: This species is recorded from South Canterbury, Ohakune, Wairakei and Lake Rotoroa, New Zealand.

PALPOMYIA NELSONI Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26: 50.

Types: Both male and female are described, but which sex is the holotype is not stated and the association of the sexes is said to be purely conjectural. In British Museum (Natural History).

Type Locality: Nelson, New Zealand.

Distribution: Nelson, Waiho and Aniseed Valley, New Zealand.

PALPOMYIA RASTELLIFER Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26: 51.

Types: Type female in British Museum (Natural History).

Type Locality: First listed locality is Lake Brunner, New Zealand.

Distribution: Recorded from Lake Brunner and Waiho, New Zealand.

PALPOMYIA URPICIFEMORIS Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26: 52.

Type: Type female in British Museum (Natural History).

Type Locality: Kaikoura, New Zealand. (Only recorded locality.)

Genus HETEROMYIA Say.

SAY, T., 1825.—*American Entomology*, 2: 79.

KIEFFER, J. J., 1906.—*Chironomidae in Wytzman's Genera Insectorum*, fasc. 42: 64.

See also—

EDWARDS, F. W., 1926.—*Trans. ent. Soc. Lond.*, 1926: 420.

MACFIE, J. W. S., 1940.—*Ann. Trop. Med. and Parasit.*, 34: 27.

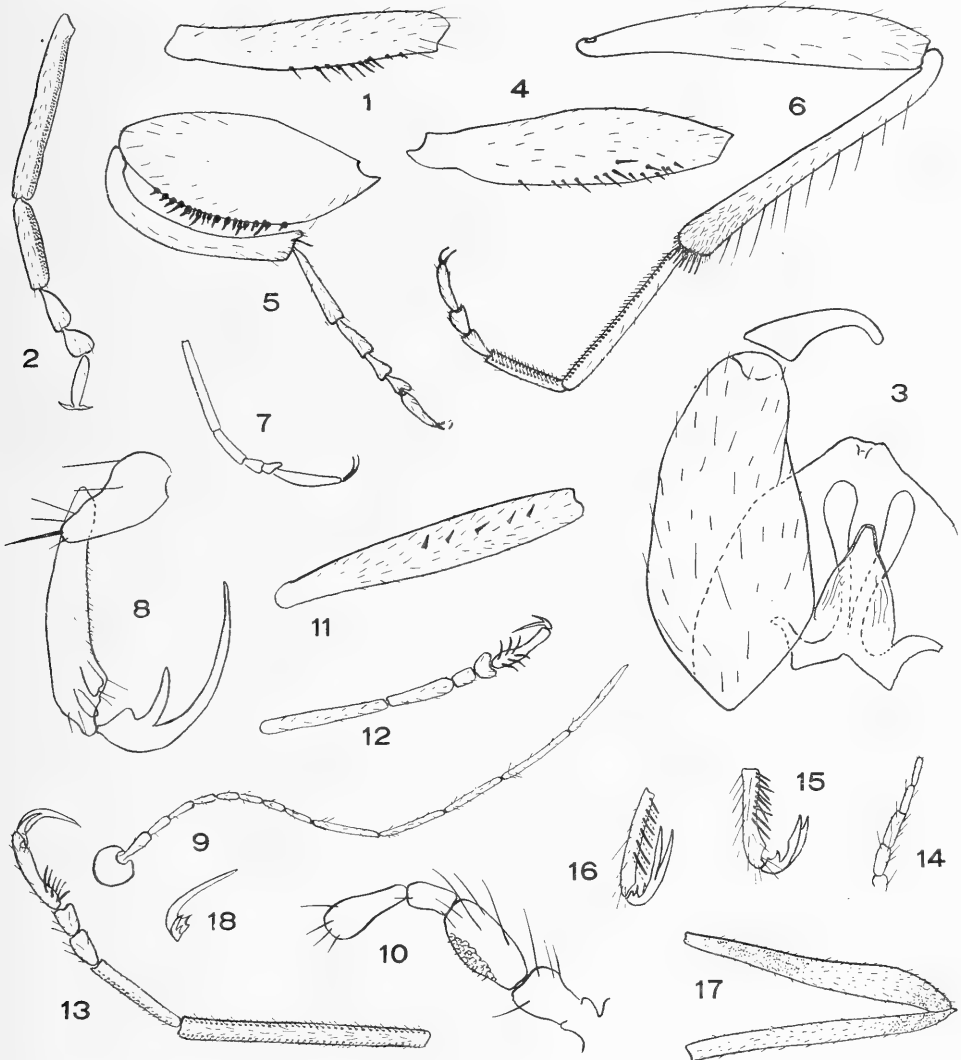
JOHANNSEN, O. A., 1943.—*Ann. ent. Soc. Amer.*, 36: 774.

Synonymy: *Pachyleptus* Walker, 1856 (vide Macfie, 1940).

Genotype: *Heteromyia fasciata* Say.

GENERIC CHARACTERS.

This genus is undoubtedly close to *Palpomymia* and is indeed included in *Palpomymia* by some authors, e.g., Edwards (1926). The chief points of difference are as follows.



Text-figures 1-17.—Various structures of species of the *Palpomymia* Group.

Figs. 1-3, *Palpomymia decima*. 1. Fore femur, $\times 52$. 2. Hind tarsus, $\times 52$. 3. Genitalia, $\times 193$.
 Fig. 4. Fore femur of *Palpomymia subalpina*, $\times 52$. Figs. 5-6, *Heteromyia tasmanica*. 5. Fore leg, $\times 52$. 6. Hind leg, $\times 52$. Figs. 7-8, *Clinohoelea tasmaniensis*. 7. Fore tarsus, $\times 38$ (swelling of fifth tarsal segment not so obvious in lateral view). 8. Last two segments of hind tarsus, $\times 193$.
 Figs. 9-13, *Xenohoelea tonnoiri*. 9. Antenna, $\times 52$ (basal segment omitted). 10. Palpus, $\times 193$.
 11. Fore femur, $\times 52$. 12. Fore tarsus, $\times 52$. 13. Hind tarsus, $\times 52$. Figs. 14-15, *Johannsenomyia australiensis*. 14. Palpus, $\times 52$. 15. Fifth tarsal segment, $\times 52$. Figs. 16-18, *Dicrohetea lalokiensis*. 16. Fifth tarsal segment of fore leg, $\times 52$. 17. Hind femur and tibia, $\times 20$ (unstippled areas yellow). 18. Fifth tarsal segment of hind leg, $\times 52$.

The femora of the fore legs are greatly swollen and armed with spines and the fore tibiae are curved to the shape of the femora. The extremities of the hind femora are distinctly clubbed in both sexes and the fourth tarsal segments on all legs of the male and on the anterior four of the female are cordate. The hind legs of the female are very long with a single long basally barbed claw but those of the anterior four legs are equal and barbed; the claws of the male are small and equal.

It is obvious that, in assigning species to *Heteromyia*, Kieffer has regarded the form of the fore femora and tibiae as of greatest importance and at times disregarded tarsal characters. This was apparently done when Kieffer described *H. brevibarba*. As I have not examined specimens of this species I feel it should be retained in *Heteromyia* until it can be studied in detail and its true generic position established. Similarly another species, *H. tasmanica*, has been included in this genus although it again does not agree with the genotype in tarsal characters but is more likely to be confused with *H. brevibarba* than with any other Australasian species in the *Palpomyia* group.

For the present then, we have two species in the genus *Heteromyia* which are similar in the character of their fore femora and tibiae but which are dissimilar in tarsi and claws; nor does either species agree with the circumscription of the genus in tarsal or unguinal characters.

If one disregards the fore femora *H. brevibarba* would probably fit into *Homohaleu* Kieffer 1917 and *H. tasmanica* would certainly be regarded as a *Palpomyia*.

HETEROMYIA BREVIBARBA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Nat. Mus. Hung.*, 15: 192.

Type: Type ♀, presumably in National Museum of Hungary, Budapest.

Type Locality: Brisbane, Queensland.

Translation of Original Description.

"♀. Black. Eyes glabrous, separated by a triangular shining space. Palpi long, second and fourth segments very short, twice as long as wide, third and fifth long. Antennae brownish black, scape and base of the eight following segments reddish-brown, segments 11-15 filiform, together twice as long as segments 3-10 together, each more than three times as long as 10, without verticels, but with sparse hairs, 4-10 cylindrical, at least twice as long as wide, with short verticels, not longer or scarcely longer than the segment. Thorax convex, higher than long, armed with a spinule at the middle of the anterior border. Mesonotum shining and glabrous. Halteres brownish black, stem pale. Wings hyaline, all the veins black, base gradually narrowing, R_{4+5} reaching at least the distal third of the wing, not passed by the costa, twice as long as R_1 , first radial cell linear, three times as long as wide, R_s very oblique, not longer than r-m, the latter perpendicular, bifurcation of M proximal to r-m, posterior branch strongly curved, curved proximally from below, distally from above, base of Cu_1 on M_{3+4} under r-m, anal vein bifurcated, intercalary fork absent. Legs dull brown, anterior femur black, two first segments of all the tarsi whitish, anterior femur very strongly thickened, armed ventrally with numerous spinules, anterior tibia curved, a little shorter than the femur and applied to it, the other four femora are long and not thickened, with one spinule in the distal third, the two posterior are feebly swollen distally into a club, posterior tibia with hairs dorsally aligned, posterior tarsus a little longer than the tibia, its first segment twice as long as the second segment, third segment scarcely as long as wide, weakly enlarged distally, fourth larger, transverse, cordiform, fifth a little longer than the third and fourth together, scarcely shorter than the second, thin, with five pairs of cylindrical black spinules; claws long, equal, attaining at least half the length of the segment, tarsi of the four other legs of the same conformation, save that in the anterior tarsus the third segment is cordiform like the fourth, the second a little shorter than the fifth, the first tarsal segment not twice as long as the following segment. Abdomen flattened, as large as the thorax, first tergite with a reddish spot. Length 3 mm."

Distribution: No further records of this species are available.

HETEROMYIA TASMANICA, n. sp.

Type: Holotype ♀ in the C.S.I.R. Museum.

Type Locality: Eaglehawk Neck, Tasmania (22: xi: 1922, A. Tonnoir).

DISTINCTIVE CHARACTERS.

A uniformly very dark brown species with very strongly swollen fore femora bearing spines on the undersurface, curved fore tibiae and fifth tarsal segments without spinules.

TABLE 2.
Various Measurements of Species of Heteromyia and Clinohoelea.

Legs.	<i>Heteromyia tasmanica</i> (Holotype).		<i>Clinohoelea tasmaniensis</i> (Holotype).	
	Wing length: 2.35 mm.		Wing length: 2.42 mm.	
	Fore Leg.	Hind Leg.	Fore Leg.	Hind Leg.
Femur	0.650 mm.	0.875 mm.	0.816 mm.	1.275 mm.
Tibia	0.540 "	0.825 "	0.765 "	1.190 "
Tarsus I	0.200 "	0.450 "	0.340 "	0.590 "
" II	0.105 "	0.200 "	0.153 "	0.272 "
" III	0.070 "	0.075 "	0.077 "	0.119 "
" IV	0.060 "	0.060 "	0.068 "	0.102 "
" V	0.105 "	0.125 "	0.221 "	0.170 "
Claw	0.050 "	0.050 "	0.102 "	0.136 "

DESCRIPTION.

(See Table 2 for measurements.)

Female.

Head: The head is very dark brown, bare except for dark orbital bristles and with the eyes narrowly separated. The antennae are dark brown with the first eight flagellar segments cylindrical and subequal and the last five also cylindrical but considerably longer, each being about twice the length of segment 10. The segments of the palpi are subcylindrical, the third being the longest and the mouthparts are less than half the height of the head.

Thorax: This is uniformly very dark brown and largely clothed with a pale grey pubescence. There is no anterior tubercle and the scutum has a sparse covering of very short black hairs largely arranged in longitudinal rows. The scutellum and postnotum are of the same colour as the rest of the thorax and the halteres have the stem brown and knob dark brown.

Legs: These are slightly lighter brown than the thorax with a reddish tinge and the first tarsal segments are lighter than the rest of the legs. The fore femora are greatly swollen (see Text-fig. 5) with stout spines on the underside for the distal two-thirds. The fore tibia is strongly arched to fit the outline of the femur. The fourth tarsus is cordate on all legs and the claws are equal and about half the length of the fifth segment. The mid and hind legs are unmodified (see Text-fig. 6).

Wings: The wings are covered with microtrichia but no macrotrichia are present. The costa extends about two-thirds of the wing length and the radial cells are well developed, the second being a little more than twice the length of the first. M is sessile.

Abdomen: This is dark brown. There are two spermathecae, the largest almost twice the size of the smaller, each with a short chitinized duct.

The male is unknown.

Distribution: Only known from the type locality.

Genus CLINOHELEA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 295 and 316.

EDWARDS, F. W., 1926.—*Trans. ent. Soc. Lond.*, 1926: 413.

Genotype (by original designation): *C. unimaculata* (Macq.).

GENERIC CHARACTERS.

This genus differs from *Palpomyia* in the following points: The fifth tarsal segments of the fore legs (in both sexes) are considerably swollen. The fourth tarsal segments (at least on the four posterior legs) are deeply bilobed and each lobe terminates in one or more stout black spines (again in both sexes). In the female the claws of the

anterior four legs may be equal or unequal but those of the hind legs are large and unequal. [Edwards (1926) mentions several other characters for this genus which are not mentioned by Kieffer in his original diagnosis and which do not apply to the Australasian species and to at least some of the species originally put into this genus by Kieffer. Hence such characters have been omitted from this diagnosis.]

Key to Australasian Species of Clinohoelea.

1. Wings with two transverse brown bands; anterior femora with four spinules on their distal halves; claws of female unequal on all legs *bifasciata* (K.)
Wings unmarked; anterior femora without spinules 2
2. Claws of female equal on four anterior legs, unequal on hind legs; femora and tibiae with yellow preapical bands *tenuissima* (K.)
Claws of female equal on two anterior legs, unequal on mid and hind legs; femora and tibiae without yellow preapical bands *tasmaniensis* n. sp.

CLINOHELEA TENUISSIMA (Kieffer).

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 195. (*Sphaeromyias*.)

———, 1917.—*Ibid.*, 15: 316. (*Clinohoelea*.)

Type: Type female presumably in National Museum of Hungary, Budapest.

Type Locality: Yomba, New Guinea.

Synonymy: *Sphaeromyias tenuissima*, Kieffer, 1917, loc. cit.

Translation of Original Description.

"♀. Black, slight and slender. Head dull reddish-brown, scarcely transverse seen from in front. Front of head and mouth-parts reddish-yellow, the latter half as long as the height of the head. Eyes separated by a linear space equalling their terminal breadth. Palpi whitish, fifth segment obtuse, longer than the fourth, with several long hairs, shorter than the third. Antennae very long and very slender, distinctly longer than the body, scape reddish-yellow, segments 3-10 whitish, 11-15 brown, the third cylindrical, twice as long as the fourth, 4-10 subcylindrical, more than four times as long as wide, 11-15 together as long as 3-10 together, filiform, each two to three times as long as 10. Thorax brilliant, glabrous, as high as long, a little convex, with a spinule at the middle of the anterior border. Halteres whitish. Wings subhyaline, scarcely lobed, veins brownish-black, R_{4+5} curved, bordering close to the wing apex, closer to the latter than M_2 , three times as long as R_1 ; first radial cell two to three times as long as wide, base of R_{4+5} very oblique, longer than r-m, the latter perpendicular; bifurcation of M proximal to r-m, situated above the base of Cu_1 on M_{3+4} . Legs slender and long, brownish-black, tarsi whitish; fore leg pale yellow, distal extremity of femur black, tibia brown with a large yellow ring before the distal extremity, the four posterior femora with a yellow ring before their distal extremities, the four posterior tibiae with a larger yellow ring distally, tarsi a little longer than the tibiae, first hind tarsus more than twice the length of the second, third segment at least twice as long as wide, fourth black in all tarsi, transverse, prolonged ventrally into two lobes which terminate in a long cylindrical black spinule, fifth segment inermous, curved, longer than the third and fourth together, strongly enlarged on the anterior tarsi, claws of all tarsi large, almost two-thirds the length of the segment, in the four anterior legs they are equal, in the two posterior legs unequal, the one slightly greater than the other. Abdomen brownish black, much more slender than the thorax, lamellae white. Length 2.5 mm."

Distribution: This species has not yet been rediscovered.

CLINOHELEA BIFASCIATA (Kieffer).

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 194 (*Palpomyia*).

———, 1917.—*Ibid.*, 15: 316 (*Clinohoelea*).

Type: Type female presumably in National Museum of Hungary, Budapest.

Type Locality: Brisbane, Queensland.

Synonymy: *Palpomyia bifasciata*, Kieffer, 1917, loc. cit.

Translation of Original Description.

"♀. Black, dull, glabrous. Vertex reddish-brown. Eyes glabrous, confluent at the vertex. Palpi long, fifth segment the longest. Antennae brownish-black, segments 3-10 reddish-brown at their bases, subcylindrical, scarcely narrowed in their distal part, 4-10 at least twice as long as wide, segments 11-15 together longer than 3-10 together, filiform, each more than twice as long as 10. Thorax higher than long, convex, with a spine at the middle of the anterior border. Scutellum reddish-brown. Halteres reddish-yellow. Wings whitish, with two transverse brown bands, of which the first extends from the anterior border to the base of Cu_1 , covering all the radius and r-m, the second joining the origin of R_{4+5} to M; R_{4+5} not passed by M_{3+4} , almost three times as long as R_1 , almost reaching the distal fifth of the wing, its base very oblique, scarcely longer than r-m, the latter perpendicular, first radial cell twice as long as wide, bifurcation of M proximal to r-m, which is also the case for the origin of Cu_1 on M_{3+4} , intercalary fork absent. Legs brown or dark brown, anterior legs with the tibiae and the other

four legs with the trochanters, the distal extremities of the femora and the tarsi a yellowish or reddish-brown; femora not enlarged, the anterior with four spinules on the distal half, the other four inermous, the two posterior legs longer than the other four, third tarsal segment transverse, in the posterior tarsi almost transverse, cordiform, the fourth transverse, cordiform, prolonged ventrally in two lobes directed forwards and each terminating in a long cylindrical black spinule; fifth segment longer than the preceding two together, inermous, in the anterior tarsi it is strongly swollen at its base; claws on all the tarsi unequal, the larger attaining two-thirds of the segment, almost three times as long as the smaller. Tergites II-V having on their posterior halves a transverse reddish-yellow band, prolonged anteriorly at the middle. Length 4 mm."

Distribution: This species has not yet been rediscovered.

CLINOHELEA TASMANIENSIS, n. sp.

Types: Holotype ♀ and one paratype ♀ in the C.S.I.R. Museum, together with a damaged but conspecific ♂ specimen.

Type Locality: National Park, Tasmania (16:xii:1922, A. Tonnoir). Paratype from Geeveston, Tasmania (7:xii:1922, A. Tonnoir).

DISTINCTIVE CHARACTERS.

A shining, dark brown species with pale whitish halteres and pale trochanters, bases of femora and first and second tarsal segments. The lack of yellow rings on femora and tibiae will distinguish this species from *C. tenuissima*.

DESCRIPTION.

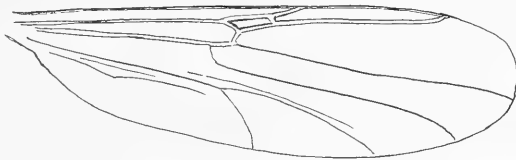
(See Table 2 for measurements.)

Female.

Head: The head is almost black, shining with the eyes rather widely separated and the mouthparts about half the height of the head. The antennae are fairly dark brown with the basal flagellar segments cylindrical and the last five elongated.

Thorax: The scutum is dark brown and shining with a very small anterior tubercle. The scutellum is not pubescent but a few border bristles are present. The halteres are whitish.

Legs: The legs are slightly lighter than the thorax with the trochanters, bases of the femora, and the first two segments of the tarsi pale brown. The femora are unmodified, the tarsi have the third segment short, the fourth bilobed, and the fifth elongate and in the fore legs this is distinctly swollen (see Text-figs. 7 and 8). The claws of the fore legs are equal, those of the mid and hind legs unequal.



Text-fig. 19.—Wing of *Clinohoelea tasmaniensis* (from holotype), × 28.

Wings: Macrotrichia are absent and the microtrichia are very fine, being barely visible at 60 ×. Text-fig. 19 illustrates the venation.

Abdomen: This is dark brown with two subequal spermathecae.

Male. The male specimen (with same collection data as the holotype) agrees in all details of colouration, but unfortunately the antennae, genitalia and fore legs are missing. However, the claws of the mid legs are equal.

Distribution: Only known from the localities listed above.

Genus XENOHELEA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 295.

MACFIE, J. W. S., 1940.—*Ann. Trop. Med. and Parasit.*, 34: 28.

Synonymy: *Mixohoelea* Kieffer, J. J., 1917. *Ann. Mus. Nat. Hung.*, 15: 364.

Genotype: *X. pruinosa* Kieffer, loc. cit. and 1918. *Ann. Mus. Nat. Hung.*, 16: 96. (By original designation.)

GENERIC CHARACTERS.

The genus has most of the characters of *Palpomyia* but the claws are unequal and simple on all legs (equal in *Palpomyia*) and the fifth tarsal segments are armed with batonnets. The eyes are rather more closely approximated than in *Palpomyia*.

Key to Australasian Species of Xenohoelea.

R_{4+5} terminating distal to level of end of M_2 *australiensis* (K.)
 R_{4+5} terminating proximal to level of end of M_2 *tonnoiri* n. sp.

XENOHELEA AUSTRALIENSIS (Kieffer).

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 364 (*Mixohoelea*).

———, 1917.—*Ibid.*, 15: 194 (*Palpomyia imparunguis*).

Type: Holotype ♀ (*Palpomyia imparunguis* K. non Becker), presumably in National Museum of Hungary, Budapest.

Type Locality: Moroka, New Guinea (1,300 m.).

Synonymy: *Mixohoelea australiensis* Kieffer loc. cit. *Palpomyia imparunguis* Kieffer loc. cit. The latter name is preoccupied by *P. imparunguis* Becker.

Translation of Original Description.

"♀. Brownish black, brilliant, glabrous. Eyes almost confluent at the vertex, separated posteriorly by a triangular space, anteriorly by a very fine line. Antennae reddish-brown, segments 11-15 brownish black, together distinctly longer than 3-10 together, filiform, each three times as long as 10, with a basal verticel of hairs longer than the other hairs, segments 4-10 subcylindrical, almost twice as long as wide. Thorax higher than long with a spinule at the middle of the anterior border. Stem of halteres pale. Wings subhyaline, strongly lobed at the base, veins brown, R_{4+5} terminating close to the wing apex, closer than M_2 , 2.5 times as long as R_1 , first radial cell two to three times as long as wide, base of R_{4+5} very oblique, a little longer than r-m, the latter almost perpendicular, bifurcation of median fork proximal to r-m, base of Cu_1 still more proximal. Legs brown, the first two tarsal segments lighter, the two hind legs longer than the other four, femora not enlarged, the anterior with four spinules on its distal half, the other four inermous, posterior tarsus a little longer than the tibia, third segment of all the tarsi not or scarcely as long as wide, fourth transverse, cordate, but not prolonged into two lobes, fifth longer than the two preceding together, equal to the second, slender, curved, fortified on its distal half with three pairs of cylindrical black spinules; claws unequal, the larger one equaling two-thirds of the segment, at least twice as long as the smaller, each with a small basal angle. Length 3 mm."

Distribution: This species has not yet been rediscovered.

XENOHELEA TONNOIRI, n. sp.

Types: Holotype ♀ and one ♀ paratype in the C.S.I.R. Museum.

Type Locality: Advent Bay, Tasmania (8 : xii: 1922, A. Tonnoir). Paratype from Geeveston, Tasmania (7 : xii: 1922, A. Tonnoir).

TABLE 3.

Various Measurements of Species of Xenohoelea and Johannsenomyia.

	<i>Xenohoelea tonnoiri</i> (Paratype ♀).		<i>Johannsenomyia australiensis</i> (Paratype ♀).	
	Wing Length, 2.47 mm.		Wing Length, 4.24 mm.	
Legs.	Hind Leg.	Hind Leg.	Hind Leg of Small Specimen. (See note in text.)	
Femur	1.248 mm.	—	—	—
Tibia	1.066 "	1.590 mm.	0.954 mm.	
Tarsus I	0.624 "	1.060 "	0.583 "	
" II	0.260 "	0.398 "	0.239 "	
" III	0.091 "	0.239 "	0.159 "	
" IV	0.052 "	0.106 "	0.079 "	
" V	0.208 "	0.265 "	0.159 "	
Claw	0.156 "	0.159 "	0.106 "	

DISTINCTIVE CHARACTERS.

This species should be easily differentiated from *X. australiensis* by the position of the end of R_{4+5} in relation to that of M_2 as detailed in the key.

DESCRIPTION.

(See Table 3 for measurements.)

Female.

Head: The head is black and shining with eyes separated dorsally. The clypeus is prominent, black and shining and the mouthparts are very short, less than half as long as the height of the head. The palpi (see Text-fig. 10) have the sensory areas of the third segments comprising many small pits. The antennae (see Text-fig. 9) are dark brown, the first eight flagellar segments are cylindrical and the last five elongated and cylindrical.

Thorax: The thorax is the same colour as the head. There is a small anterior tubercle on the anterior margin of the scutum and the latter is clothed with brown pubescent hairs. The pleura are shining or if viewed obliquely appear covered with a fine, greyish bloom. The scutellum is covered with brown pubescent hairs and a few dark brown border bristles and the halteres are dark brown with lighter brown stems.

Legs: The coxae are reddish-brown to dark brown, the femora and tibiae dark brown, shining and the fore femora (Text-fig. 11) have five or six short strong spines on the undersurface. The first two tarsal segments are yellowish, but the third to fifth segments are dark brown. The fourth tarsal segments are cordate, the bases of the fifth segments are armed ventrally with a group of six strong spinules. The tarsal claws are single, curved and each with a basal tooth, the major branch being about two-thirds the length of the fifth segment (see Text-fig. 12 for illustration of fore tarsus and Text-fig. 13 for hind tarsus).

Wings: Microtrichia are present over the wing surface but macrotrichia are absent. The venation is shown in the photograph (Plate v, fig. 3).

Abdomen: The abdomen is dark brown but rather dull and there are two subequal spermathecae.

Distribution: Apart from the specimens from Tasmania listed above I have before me a series of eight specimens from the vicinity of Canberra (Blundell's, A.C.T., 7:i:1930, A. Tonnoir; Blundell's, A.C.T., 15:iii:1930, L. F. Graham), two of which agree quite well with the holotype but are a little smaller, and the rest are very similar, the only apparent differences being their slightly smaller size and the colouration of the femora and tibiae. Instead of being uniformly dark brown the fore and mid femora are reddish-brown and only very dark at the apex and the hind femora are dark near the base and the apex with a central reddish-brown area. The tibiae are also reddish-brown and only very dark at the base and the apex in the fore and hind tibiae, the latter particularly. In this group I am loath to place any reliance on small size differences and the fact that the Canberra series is not constant in colouration makes it advisable to consider these specimens, for the present at least, as *X. tonnoiri*.

Genus JOHANNSENOMYIA Malloch.

MALLOCH, J. R., 1915.—*Bull. Illin. State Lab.*, 10: 332.

EDWARDS, F. W., 1926.—*Trans. ent. Soc. Lond.*, 1926: 413.

Synonymy: *Johannseniella* auct. partim; *Sphaeromyias*, Kieffer nec Curtis (see Macfie, 1940).

Genotype: I have not been able to discover what species constitutes the genotype of *Johannsenomyia*.

GENERIC CHARACTERS.

Johannsenomyia is similar to *Palpomylia* except that there is no trace of an anterior tubercle; all the femora are unarmed; the fifth tarsal segments of the female have two rows of batonnets on the undersurface and the claws of the female are equal with a large tooth at the base of each.

Only one species from Australia can as yet be ascribed to this genus.

JOHANNSENOMYIA AUSTRALIENSIS, n. sp.

Types: Holotype ♀ and three ♀ paratypes in the C.S.I.R. Museum.

Type Locality: Cotter River, Australian Capital Territory (14:xii:1929, A. Tonnoir).

DESCRIPTION.

(See Table 3 for measurements.)

Female.

Head: The head is black, the eyes are divided and the clypeus is large and prominent, black and shining. The length of the mouthparts is little more than half the height of the head. The pedicels and the basal halves of the third segments of the antennae are brown, the rest dark brown. The first flagellar segment is twice as long as the following seven segments, all are elongated and slightly tapered distally; the last five segments are more elongated, each being about twice the length of segment 10. The verticils are short, not dense. The palpus is illustrated in Text-fig. 14.

Thorax: This is uniformly black. There is no anterior tubercle or spine and the scutum is shiny and sparsely pubescent. The scutellum is black and shining and the halteres are black with dark brown stems.

Legs: The femora and tibiae are very dark brown, the tarsi rather reddish-brown. The fore femora are not swollen or spinose. The fourth segments of the tarsi are small and the fifth armed with blunt spines (see Text-fig. 15). The claws are fairly long, about two-thirds the length of the fifth segment, equal and each with a small basal tooth.

Wings: Macrotrichia are absent but microtrichia are present over the whole surface. The venation is illustrated in the photograph in Plate v, fig. 2.

Abdomen: This is very dark brown, without gland rods and with three spermathecae, the dimensions of which are $85\mu \times 75\mu$, $80\mu \times 65\mu$ and $25\mu \times 25\mu$, the last having a duct 10μ long.

Distribution: This species is only known from the type locality. Note: Apart from the specimens listed as types there are three other females with exactly the same collection data which agree with the holotype in all respects except size. These specimens are distinctly smaller (e.g., the wing length is 2.4 mm. as compared with 4.2 in the holotype). Nevertheless I feel that they must still be considered to be *J. australiensis*.

Genus DICROHELEA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 363.

MACFIE, J. W. S., 1940.—*Ann. Trop. Med. and Parasit.*, 34: 27.

Genotype: *D. flicornis* (Kieffer). Originally described by Kieffer in *Palpomyia* (Kieffer, 1910, p. 196). Of the five species originally placed in this genus by Kieffer, *D. flicornis* is the first mentioned and has been accepted by Macfie (1940) as the genotype.

GENERIC CHARACTERS.

This genus is closely related to *Palpomyia*, differing particularly in the tarsi. The claws of the fore legs are equal and bifid, the median tooth being very long and the lateral tooth very short. On the four posterior legs the claws are unequal and bifid, one with the median tooth very long and the lateral tooth very short, the other with the median tooth short and the lateral tooth very short. The fourth tarsal segments are cylindrical, not cordiform and the fifth tarsal segments are armed with black batonnets.

Only one species has so far been found in the Australasian Region.

TABLE 4.

Various Measurements of Dicrohelea lalokiensis.
Wing length, 3.23 mm.

Antenna.		Legs.	Fore Leg.	Hind Leg.
Segment	3 .. 0.136 mm.	Femur.	1.219 mm.	1.855 mm.
Segments 4-10, each	0.085 "	Tibia.	1.272 "	1.749 "
Segment	11 .. 0.357 "	Tarsus I.	0.530 "	1.370 "
"	12 .. 0.340 "	" II.	0.265 "	0.424 "
"	13 .. 0.289 "	" III.	0.137 "	0.212 "
"	14 .. 0.289 "	" IV.	0.080 "	0.159 "
"	15 .. 0.272 "	" V.	0.318 "	0.292 "
		Claw.	0.212 "	0.265 "

DICROHELEA LALOKIENSIS, n. sp.

Types: Holotype ♀ and two ♀ paratypes in the C.S.I.R. Museum, Canberra, A.C.T.

Type Locality: All three specimens were taken on the bank of the Laloki River, at the foot of the pass to Sogeri, Papua (2: vi: 47, D. J. Lee).

DISTINCTIVE CHARACTERS.

Until other species of this genus are found in the region the distinctive characters remain those of the genus itself.

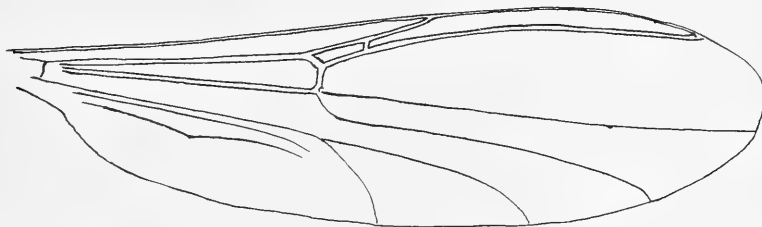
Description: Female. (See Table 4 for measurements.)

A large shining black species with partly yellow head and some yellow markings on legs.

Head: This is brown dorsally but the clypeus and mouthparts are yellow and the palpi brown. The antennae have light brown pedicels, segments 3-10 are yellowish with a narrow dark ring at their apices and segments 11-15 are brown. Segment 3 is longer than 4, all flagellar segments are cylindrical but 11-15 are greatly lengthened. The eyes are narrowly but distinctly separated.

Thorax: An anterior tubercle is present on the scutum. The thorax is entirely shining black except for yellow-brown pronotal lobes and similar fore coxae although on these the upper anterior surface is darker brown. The halteres are black with the basal part of the stem whitish.

Legs: There are no spines on the femora but the posterior pair are swollen preapically. The anterior femora are yellow except for a brownish base and a narrow black apex, the mid and hind femora (Text-fig. 17) are black for the basal half, then there is a broad yellow band followed by a black apex. (In the paratypes the yellowish colouration is restricted in varying degree but in the darkest specimen a narrow preapical yellowish band is still present.) The basal fourth of the tibiae is black, the rest yellow. (In the other specimens this varies to almost entirely black but the apex is still yellow.) The first and second tarsal segments are yellow with a narrow dark apex, the third is pale at the base, the rest brown, the fourth and fifth are brown and the claws black. Tarsus 4 is shorter in the four anterior legs than in the hind legs and tarsus 5 is elongate with about seven pairs of strong, black spinules. The claws are equal and toothed on the fore-legs (Text-fig. 16) and very unequal and toothed on the four posterior legs (Text-fig. 18).



Text-fig. 20.—Wing of *Dicrohelea lalokiensis* (from holotype), $\times 30$.

Wings: These are hyaline, macrotrichia are absent and microtrichia cannot be seen at $\times 60$. The costa, the radius, the base of M and r-m are strong and brown, the rest of the veins are weaker and pale. The costa and R_{4+5} terminate beyond the level of the end of M_2 . There are two radial cells, the second being very long and M_2 is scarcely sessile. The venation is illustrated in Text-fig. 20.

Abdomen: This is long, narrow, and shining black.

Male Genitalia: Attached to the female type were found the genitalia of a male broken off during copulation. They were removed and mounted with the holotype but were found to be rather too broken for accurate description. However, the mount will undoubtedly prove useful for comparison with any suspected males of this species which may be collected in the future.

Distribution: Only known from the type locality.

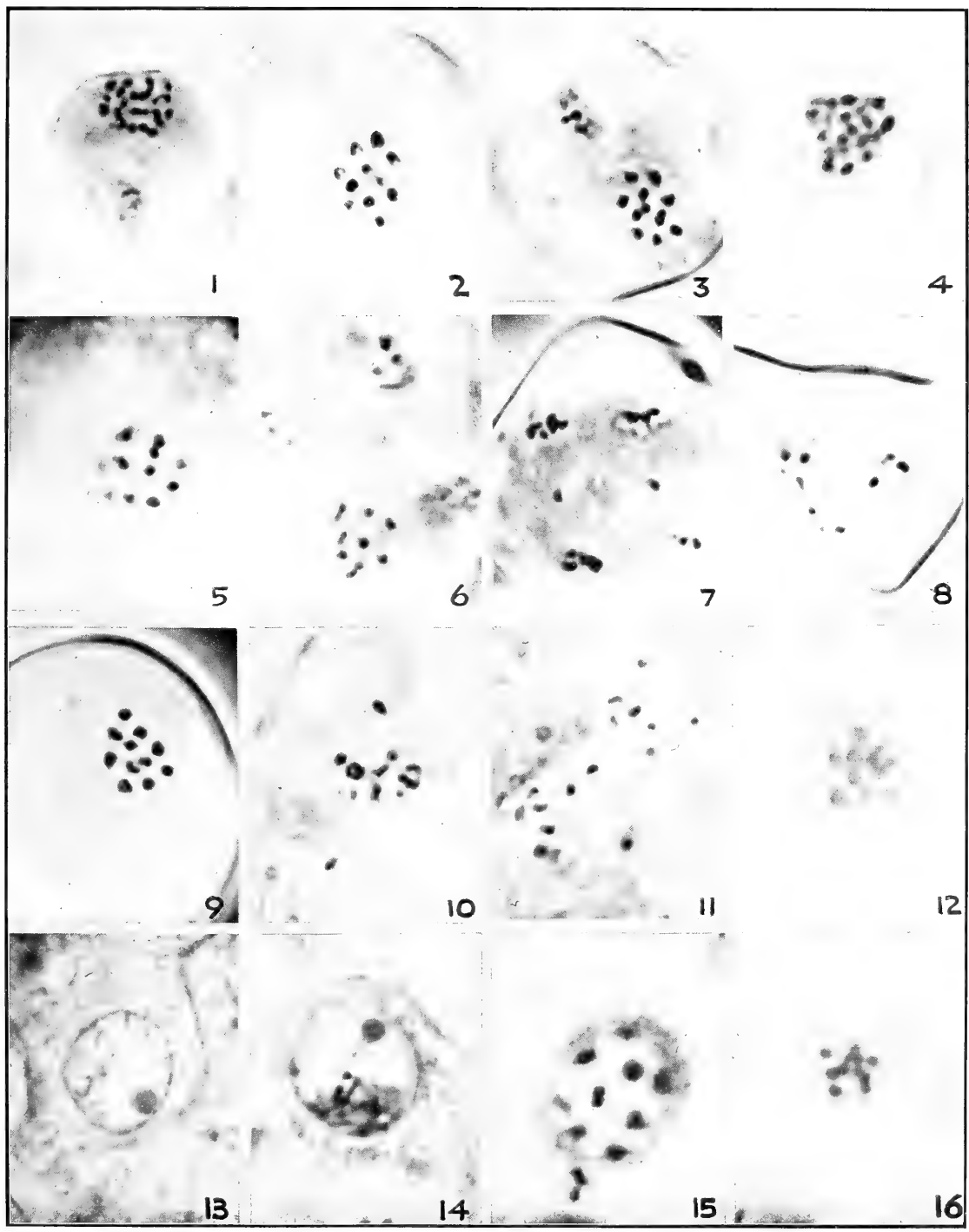
References.

Systematic references are cited in full in the text; for other general references not listed here see Part I of this series.

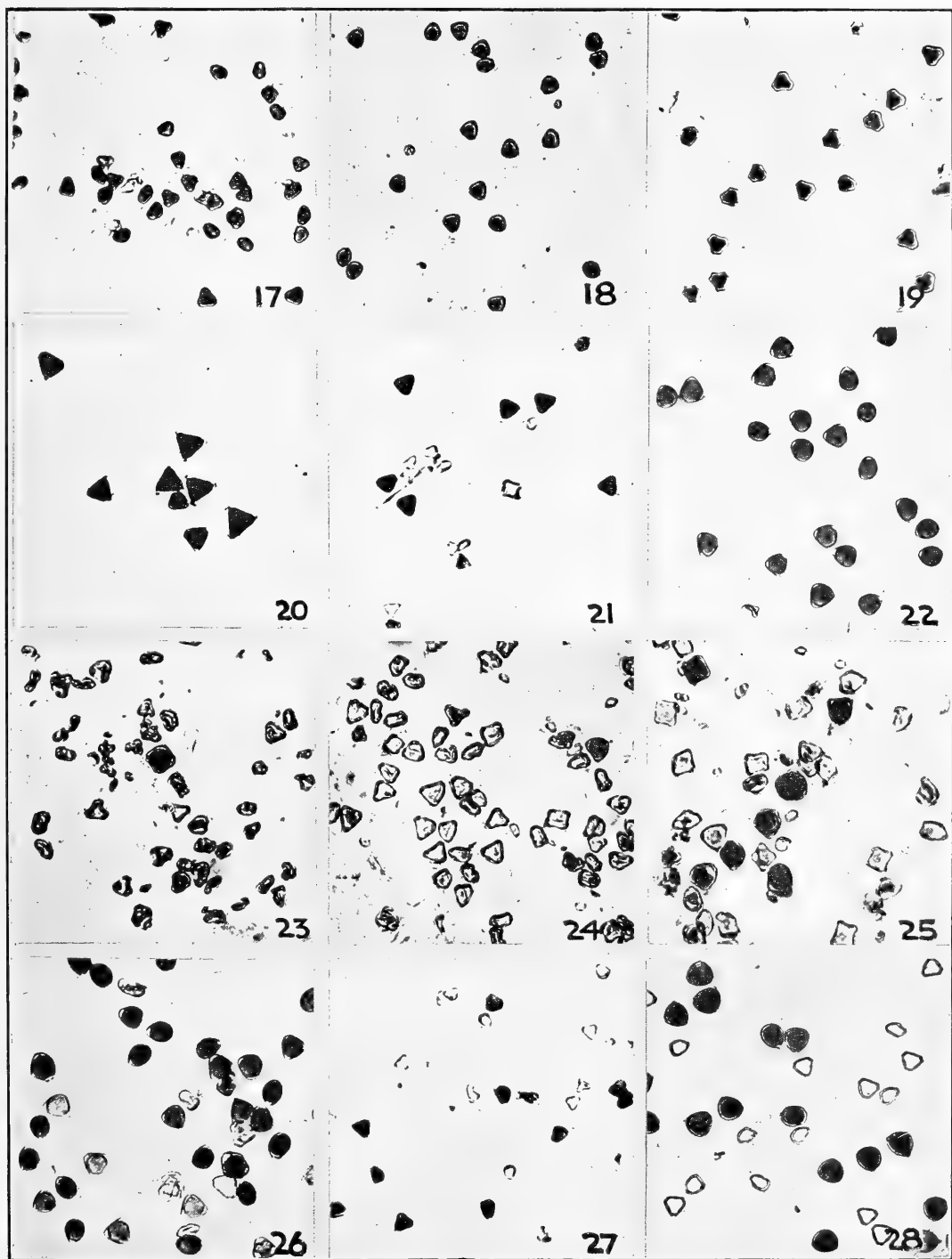
EXPLANATION OF PLATE V.

Photographs of wings of various species of the *Palpomyia* group. All $\times 25$.

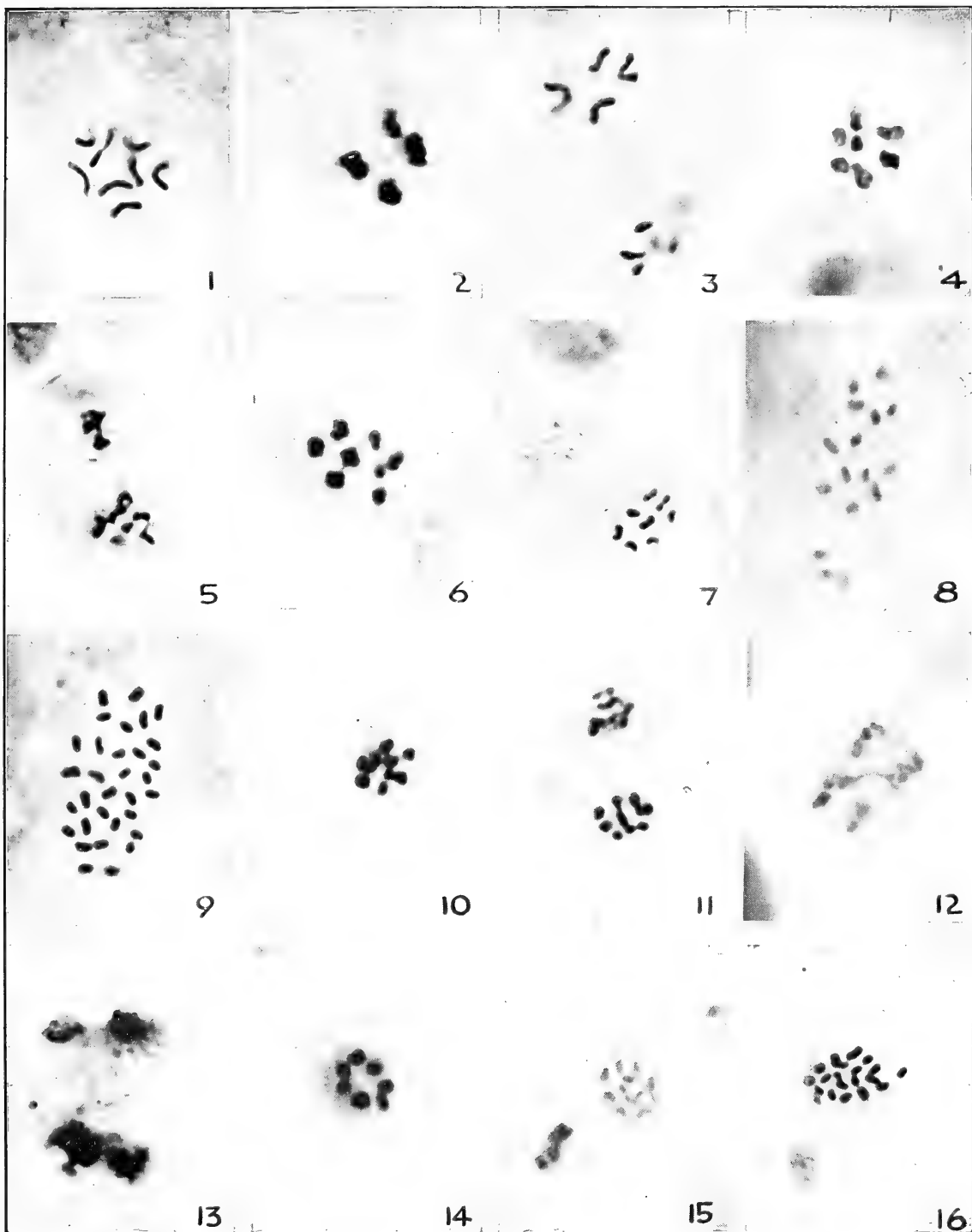
1. *Palpomyia decima* (holotype). 2. *Johannsenomyia australiensis* (paratype). 3. *Xenochelea tonnoiri* (paratype).



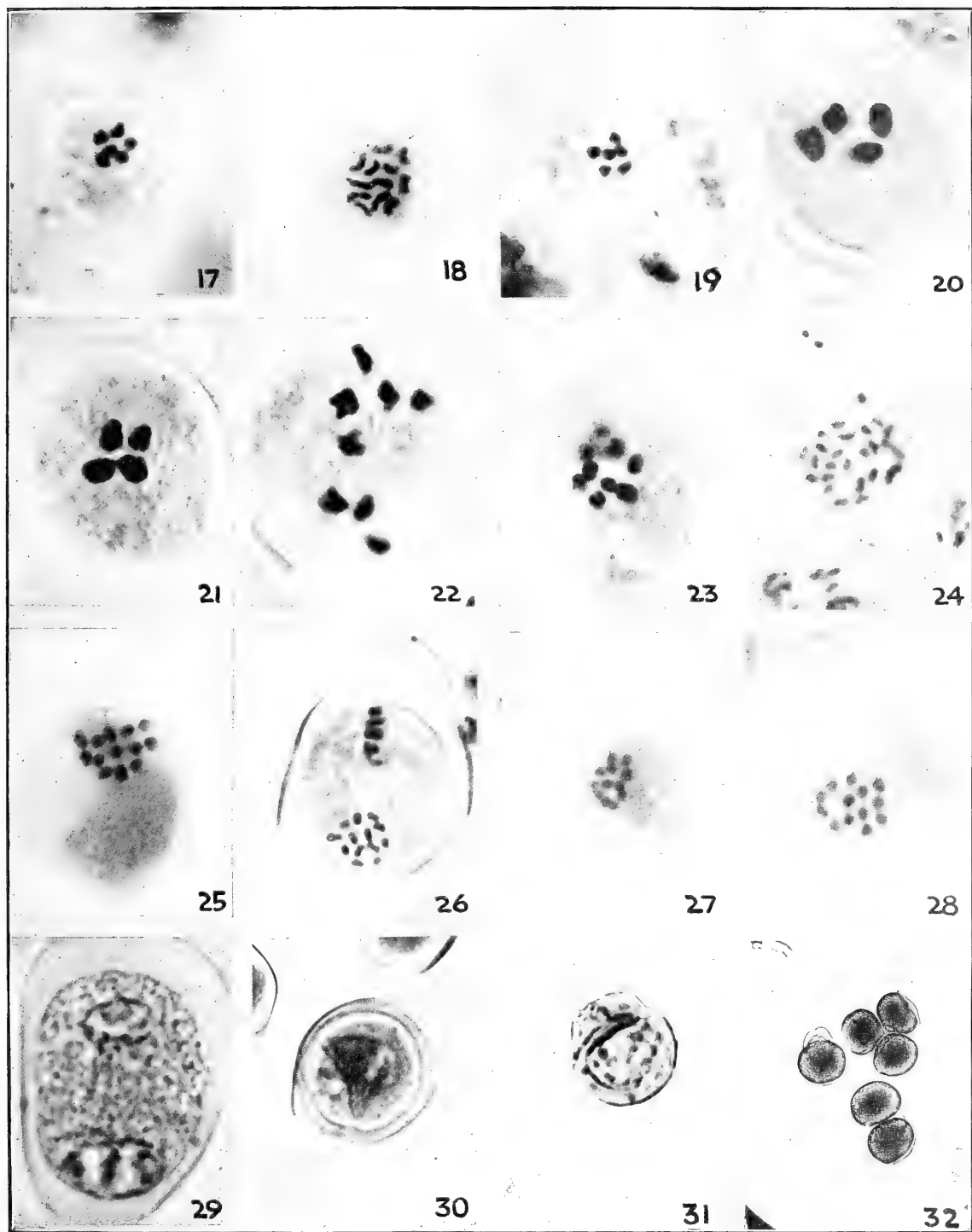
Cytology of the Myrtaceae.



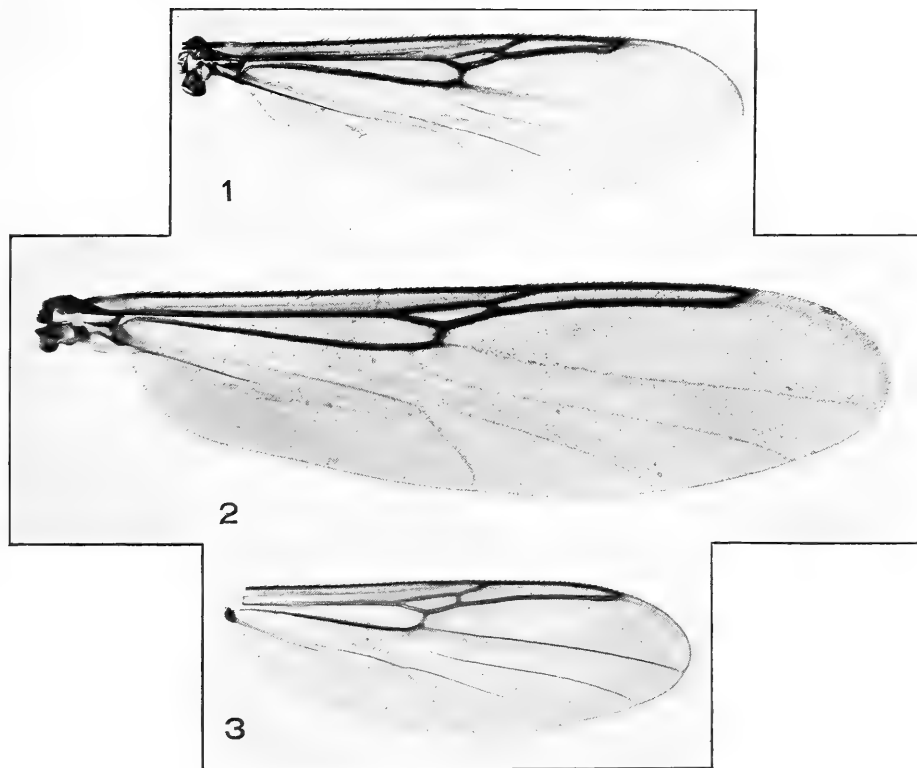
Pollen of the Myrtaceae.



Cytology of the Epacridaceae.



Cytology of the Epacridaceae.



Australasian Ceratopogonidae. Part V.

THE ANOPHELINE MOSQUITOES OF NORTH-WEST BORNEO.

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(With twenty Text-figures.)

[Read 26th May, 1948.]

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INTRODUCTION.

During the period June, 1945, to January, 1946, the author, as a member of the Australian Military Forces, was engaged in field investigations of the Anopheline species of North-West Borneo. During this work it was found that the literature was almost devoid of references to the local Anopheline fauna and, moreover, certain of the species were found to show morphological peculiarities which seemed worthy of further study. A collection, as representative of the area as possible, was therefore made for later, more detailed examination. The following pages record the results of such examination, carried out in the Faculty of Agricultural Science, University of Sydney.

The aim of this paper is to set out a reasonably detailed account of the principal systematic characters of the Borneo species and to indicate the chief characters by which they may be identified. Although descriptions of most of the species are available from other countries, these contain much detail applicable only to the country concerned, and may differ from those from other areas. In some cases, too, the Borneo specimens differed from those described from any other area, and it was therefore

decided to record the observations *in toto* for all species. The reliability of the following descriptions, however, is variable, as the numbers examined were small in some cases and cannot be considered truly representative of the area; the actual number of specimens examined is therefore stated for each species. It must also be stressed that the area treated includes only the coastal strip of Borneo, from the Miri oilfields in Sarawak, to Jesselton in British North Borneo, and can scarcely be considered typical of the entire island.

An attempt has also been made to analyse the distribution and morphology of the species described, to determine their relationship to the same or similar species in other countries in the light of modern views on the process of speciation. The Borneo fauna offers interesting possibilities in this regard, showing features of both the rather distinctive Philippine fauna and that of the Netherlands East Indies and Malaya. In some species, definite evidence of subspeciation can be seen, but in only one case was it considered advisable to establish formally a new subspecies.

PREVIOUS RECORDS.

The voluminous literature dealing with Oriental Anophelines contains few references to the fauna of British Borneo. From the much larger Dutch Borneo we have more information, and Swellengrebel and Rodenwaldt (1932) give a number of references to records of Borneo species. However, apart from the paper by Walch and Soesilo (1929), little attention appears to have been paid to the Borneo fauna as a separate entity.

From the British colonies in N.W. Borneo have come only six papers on the Anophelines found there, those by Roper (1914), Moulton (1914), Stookes (1924, 1927), Scharff (1927), and McArthur (1946). (Most of the valuable and detailed work of the latter author has not yet been published.)

Roper (1914) recorded ten species from British North Borneo, including a description of *A. brevivalpis*, n. sp., together with biological data on breeding grounds and vector potentialities and a certain amount of systematic data. Dissections are recorded to show *A. umbrosus* as a vector species, and epidemiological evidence to cast suspicion on *A. leucosphyrus*. In the same year Moulton (1914) published a list of twelve species of Borneo Anophelines, in the collection of the Sarawak Museum. The next papers, by Stookes (1924, 1927), record ten species from the Miri oilfields and deal mainly with details of biology and control. In these *A. "ludlowi"* (*sundaicus*) is incriminated as a vector, and further epidemiological evidence offered to incriminate *A. leucosphyrus*. The paper by Scharff (1927) records seven species found in a survey of Labuan Is., with data on breeding grounds, and epidemiological evidence of vector efficiency, and concludes that *A. ludlowi* (*sundaicus*) is the principal vector of the island. The last paper, by McArthur (1946), is a preliminary account of a large amount of evidence, definitely incriminating *A. leucosphyrus* as a dangerous vector in the interior of Borneo.

The species recorded from Borneo are shown in the list below, authors being indicated as follows: 1. Roper (1914). 2. Moulton (1914). 3. Stookes (*a*, 1924; *b*, 1927). 4. Scharff (1927). 5. McArthur (1946 and unpublished). 6. Swellengrebel and Rodenwaldt (1932). 7. This paper. Records marked "?" are considered doubtful and possibly refer to another species or subspecies; those marked "??" have been interpolated as the probable identity of records made under another name.

Subgenus ANOPHELES Meigen.

Group *Anopheles* Root.

Series *Anopheles* Edwards.

1. *aitkenii* James 6, 7
2. *palmatus* Rodenwaldt 6
3. *brevivalpis* Roper 1, 2, 3b, 7

Series *Myzorhynchus* Edwards.

4. *albotaeniatus* Theobald .. 1, 2, 3b, 6, 7
5. *barbirostris* van der Wulp
..... 1, 2, 3a, 3b, 4, 6, 7

6. *barbumbrosus* Strickland and Chowd-
hury 7

7. *montanus* Stanton and Haçker 6

8. *hyrcanus nigerrimus* Giles
..... 4??, 6??, 7

9. *hyrcanus sinensis* Wiedemann
..... 2?, 3a?, 3b?, 4?

10. *hyrcanus* "nr. *sinensis*" 7

11. *separatus* Leicester .. 1, 2, 3b, 4, 6, 7

12. *baezi gateri* Baisas 7

13. *umbrosus* Theobald
..... 1, 2?, 3a?, 3b?, 4?, 6?, 7

- 14. sp. *A* nr. *umbrosus* 1??, 7
 - 15. sp. *B* nr. *umbrosus* 6??, 7
- Subgenus *MYZOMYIA* Blanchard.
- Group *Neomyzomyia* Christophers.
- 16. *kochi* Donitz 1, 2, 3*b*, 4, 6, 7
 - 17. *tessellatus* Theobald .. 1, 2, 3*a*, 3*b*, 6, 7
 - 18. *leucosphyrus leucosphyrus* Donitz ...
..... 1?, 2?, 3*a*?, 3*b*?, 5?, 6?
 - 19. *leucosphyrus balabacensis* Baisas .. 7
 - 20. *leucosphyrus pujutensis* n. subsp. .. 7
 - 21. *hackeri* Edwards 6?
- Group *Myzomyia* Christophers.
- 22. *aconitus* Donitz 6

- Group *Pseudomyzomyia* Christophers.
- 23. *litoralis* King 5?
 - 24. *hulldowi* Theobald ... 1?, 2?, 3*b*?, 4?, 5
 - 25. *subpictus* Grassi 6
 - 26. *sundaicus* Rodenwaldt
..... 1??, 2??, 3*b*??, 4??, 6, 7
 - 27. *vagus vagus* Donitz 4?, 6
 - 28. *vagus limosus* King 7
- Group *Neocellia* Christophers.
- 29. *karwari* James 2, 4, 6, 7
 - 30. *maculatus* Theobald 1, 2, 5, 6, 7
 - 31. *annularis* van der Wulp 6?
 - 32. *errabundus* Swellengrebel 6
 - 33. *philippinensis* Ludlow 7

ABBREVIATIONS AND NOMENCLATURE.

Taxonomic terms used in the following descriptions follow those of Christophers (1933), retaining for convenience the numeral system of nomenclature of the wing veins. The following abbreviations have been used throughout:

*Adult.**

- pn. l. pronotal lobes
- pr. s. propleural setae
- ust. s. upper sternopleural setae
- lst. s. lower sternopleural setae
- sp. s. spiracular setae
- um. s. upper mesepimeral setae
- pa. s. prealar setae
- tarsus, 1-5 tarsal segments 1-5
- abd. I-VIII .. abdominal segments I-VIII
- af. anterior fork cell
- pf. posterior fork cell

Larva.

- ic. inner anterior clypeal hairs
- oc. outer anterior clypeal hairs
- pc. posterior clypeal hairs
- sut. sutural hairs
- t. sut. trans sutural hairs
- is. inner shoulder hairs
- cs. central shoulder hairs
- os. outer shoulder hairs
- ppl. prothoracic pleural group
- mpl. mesothoracic pleural group
- mtpl. metathoracic pleural group
- mt. palm metathoracic palmate hair
- psp. post-spiracular hair
- abd. I-VIII .. abdominal segments I-VIII

KEY TO THE ANOPHELINE MOSQUITOES OF BORNEO.

The following keys, based on those given by Russell, Rozeboom, and Stone (1943), are designed to enable reasonably accurate identification of female and larval specimens of Borneo Anopheline. Individual specimens may, however, occasionally vary beyond the limits given below, and for definite identification, a check should be made against the fuller descriptions. This is particularly important when using the larval key, where it will be found that the species in certain groups cannot be separated on key characters. In all doubtful cases a definite identification should not be made until the larva has been bred through to the adult stage. All species treated in this paper are included in the keys, together with certain others recorded from, or possibly occurring in, Borneo. For descriptions of species not treated in this paper, reference can be made to Gater (1934 and 1935), Swellengrebel and Rodenwaldt (1932), Christophers (1933), and Russell and Baisas (1934 and 1936).

A. ADULT FEMALES.

- 1. Wing not spotted 2
- Wing spotted 4
- 2. Wing scales brown, dark 3
- Wing scales yellow, light *A. vagus* (= *immaculatus*)
- 3. Palps about three-quarters length of labium; large species *A. brevipalpis*
- Palps as long as labium; small species *A. aitkenii aitkenii*, *A. aitkenii bengalensis*,
A. palmatus, *A. insulaeflorum*.
- 4. Wing with less than four dark areas involving both costa and vein 1 5
- Wing with at least four dark areas involving both costa and vein 1 18
- 5. Palps with distinct pale bands or markings 6
- Palps uniformly dark or with, at most, a few scattered pale scales 11
- 6. Abdominal segment VII with a tuft of scales ventrally; clypeus with lateral scale tufts 7
- Abdominal segment VII and clypeus without scale tufts 10

* In all illustrations, structures shown are those of the adult female, unless otherwise indicated.

7. Hind tarsal segments 4 and 5 not both completely white 8
 Hind tarsal segments 4 and 5 both completely white *A. hyrcanus nigerrimus*
 (form *argyropus*).
8. Wing with apical fringe spot from apex of vein 1 to past apex of vein 3; coxae with
 scales 9
 Wing with apical fringe spot from apex of vein 1 to apex of vein 2 only; coxae without
 scales *A. hyrcanus* subsp. near *sinensis*
9. Hind tarsal segment 4 pale at apex only; wing with subcostal spot equally involving
 vein 1 *A. hyrcanus sinensis*
 Hind tarsal segment 4 pale at base and apex; subcostal spot only partially or not,
 involving vein 1 *A. hyrcanus nigerrimus*
10. Hind tarsal segment 5 completely white; any pale scales on palps restricted to narrow
 areas 12
 Hind tarsal segment 5 not completely white; pale scales on palps forming broad bands
 *A. separatus*, *A. hunteri*
11. Hind tarsal segment 5 completely white 12
 Hind tarsal segment 5 not completely white 13
12. Hind tarsal segments 3 and 4 each at least half white *A. albotaeniatus*
 Hind tarsal segments 3 and 4 each only tipped with white at base and apex .. *A. montanus*
13. Abdominal segment VII with a tuft of scales ventrally; basal third of costa with some
 scattered pale scales 14
 Abdominal segment VII and costa not as above 15
14. Wing with small pale fringe spot at apex of vein 3, sometimes one at 2-1; abdomen usually
 with some pale scales ventrally *A. barbirostris*
 Wing with large pale fringe spot from apex at vein 2-2 or 3 to apex of 4-1; abdomen without
 pale scales ventrally *A. barbumbrosus*
15. Hind tarsal segments without pale markings *A. baezai gateri*
 Hind tarsal segments with distinct pale bands 16
16. Propleural hairs present; front tarsi with definite pale bands
 *A. umbrosus* (syn. *novumbrosus*)
 Propleural hairs absent; front tarsi with minute pale bands or none 17
17. Coxae without scales; 4-6 upper sternopleural hairs present .. *A. sp. "A"* near *umbrosus*
 Coxae with scales; more than 10 upper sternopleural hairs present. *A. sp. "B"* near *umbrosus*
18. Hind tarsal segment 5 partially or entirely white; some other tarsal segments white or
 with conspicuous pale bands 19
 Hind tarsal segment 5 entirely or mainly dark; other tarsal segments dark or with only
 narrow pale bands 30
19. Legs with femora and tibiae not speckled 20
 Legs with femora and tibiae speckled 25
20. Hind tarsal segments 4 and 5 white; apex of segment 3 sometimes white; palps with three
 pale bands 21
 Hind tarsal segment 4 with a black band; palps with 4 pale bands *A. karwari*
21. Vein 5 with stem and lower branch mostly pale, without any dark spot at origin of 5-1 .. 22
 Vein 5 with stem and lower branch mostly dark or at least with a dark area at origin
 of 5-1 *A. annularis*
22. Hind tarsal segments 3, 4, and 5 white, sometimes segment 2 white apically; palps with
 pale apical band not more than half as wide as dark pre-apical band 23
 Hind tarsal segment 3 only half white; palps with pale apical band more than half as
 wide as pre-apical dark band and involving half or more of segment 4 .. *A. schuffneri*
23. Abdomen with scattered scales ventrally on most segments, and dorsally on segments V
 and VI; sternopleura with defined patches of pale scaling; hind tarsal segment I with
 or without an apical pale area 24
 Abdomen with few or no pale scales except apically on venter and dorsum; sternopleura
 without defined patches of pale scaling; hind tarsal segment with an apical pale
 area *A. philippinensis*
24. Abdomen laterally with prominent tufts of dark scales visible from above on segments II
 to VII; palps with scattered pale scales on dark areas of segments 3 and 4; hind tarsal
 segment 1 with apical pale area *A. errabundus* (= *philippinensis*?)
 Abdomen and palps not as above; hind tarsal segment 1 never with pale apical spot
 *A. pallidus*
25. Abdomen without conspicuous ventral scale tufts 26
 Abdomen with conspicuous ventral tufts of dark scales on segments II to VII .. *A. kochi*
26. Vein 6 with more than three dark spots 27
 Vein 6 with two or three dark spots *A. maculatus*
27. Hind leg with broad white band involving both sides of tibio-tarsal joint 28
 Hind leg without such band *A. tessellatus*
28. Palps much shorter than proboscis, with very narrow pale bands *A. hackeri*
 Palps as long as or slightly shorter than proboscis, with normal bands 29

29. Proboscis uniformly dark, equal in length to palps; presector dark spot of vein 1 usually divided into two or three small dark spots *A. leucosphyrus balabacensis*
 Proboscis with narrow apical golden band or tache, and slightly longer than palps; presector dark spot of vein 1 undivided *A. leucosphyrus pujutensis*
30. Fore tarsi segments with broad pale bands at joints 31
 Fore tarsal segments with narrow or no pale bands at joints 29
21. Femora and tibiae speckled 32
 Femora and tibiae not speckled 36
32. Vein 6 with two or three dark spots 33
 Vein 6 with more than three dark spots 27
33. Wing fringe with nine or ten large pale spots at apices of veins and between veins 5-1 and 5-2, and 5-2 and 6 *A. parangensis*
 Wing fringe with seven or eight small spots at apices of veins and sometimes between veins 5-2 and 6 34
34. Wing with two dark spots on vein 1 below median dark area of costa 35
 Wing with three dark spots on vein 1 below median dark area of costa *A. ludlowi*
25. Costa usually with pale scaling anteriorly in prehumeral area, but often lacking sector pale spot; fringe spot usual between veins 5-2 and 6 *A. litoralis*
 Costa without pale scaling in prehumeral area; sector pale spot usually present; no fringe spot between veins 5-2 and 6 *A. sundaicus*
36. Apical pale band of palps not more than twice as wide as pre-apical dark band; costa with prehumeral area dark or with pale spots 38
 Apical pale band of palps three or more times as wide as pre-apical dark band; costa with prehumeral area entirely dark or with some pale scales anteriorly 37
37. Proboscis with pale tache towards apex *A. vagus vagus*
 Proboscis uniformly dark, without tache *A. vague limosus*
38. Palps with apical pale band only as wide as pre-apical dark band; costa usually with pale scaling in prehumeral area *A. subpictus subpictus*
 Palps with apical pale band about twice as wide as pre-apical dark band; costa without pale scaling in prehumeral area *A. subpictus malayensis*
39. Palps with apical and sub-apical pale bands as wide as or wider than intervening dark band 40
 Palps with sub-apical pale band much narrower than pre-apical dark band .. *A. fluviatilis*
40. Wing usually without fringe spot at vein 6; labium pale on apical half 41
 Wing with fringe spot at vein 6; labium pale on apical half *A. aconitus*
41. Costa entirely dark on basal third; labium pale on apical half *A. varuna*
 Costa with pale interruption (sometimes very small) on basal third; labium uniformly dark or with small pale ventral area .. *A. minimus* (including *A. minimus flavirostris*)

B. FOURTH INSTAR LARVAE.

1. Inner clypeal hairs approximated, the distance between their bases not more than the distance between the bases of inner and outer clypeal hairs on one side; antennal hair branched 2
 Inner clypeal hairs placed far apart, the distance between their bases twice or more the distance between the bases of inner and outer clypeal hairs on one side; antennal hair simple 15
2. Some abdominal palmate hairs with well-developed leaflets 3
 Abdominal palmate hairs with filamentous branches only 4
3. Abdominal palmate hairs with leaflets on at least segments 3 to 7 8
 Abdominal palmate hairs with leaflets on segments 4 to 6 only *A. umbrosus* (syn. *novumbrosus*)
4. Posterior clypeal hairs simple or divided at the base into two or three branches 5
 Posterior clypeal hairs usually with distinct stem and two or three branches distally *A. brevipalpis*
5. Posterior clypeal hairs simple 6
 Posterior clypeal hairs two- to four-branched from near base .. *A. sp. "A"* near *umbrosus*
6. Lateral hairs of abdominal segment IV with not more than five branches 7
 Lateral hairs of abdominal segment IV with six to twelve branches *A. baezai gateri*
7. Trans-sutural hair two to three branches; antennal hair 7- to 13-branched .. *A. hunteri*
 Trans-sutural hair four to eight branches; antennal hair 17- to 36-branched .. *A. separatus*
8. Anterior tergal plates very large, occupying nearly or more than half the dorsum of each segment *A. palmatus*
 Anterior tergal plates small except on segment VIII 9
9. Antennal hair small, less than half the length of the shaft; outer clypeal hairs simple or with not more than five branches, not bushy 10
 Antennal hair large, half or more the length of the shaft; outer clypeal hairs bushy with at least six branches, usually many more 11
10. Inner clypeal hair simple; lateral hair on abdominal segment 3 with five to eight branches *A. insulaeflorum*
 Inner clypeal hair usually with side hairs or branches; lateral hair on abdominal segment 3 with more than eight branches *A. aitkenii aitkenii*, *A. aitkenii bengalensis*

11. Inner clypeal hairs with bases nearly touching 12
 Inner clypeal hairs with bases nearly as far apart as the distance between inner and outer clypeal hairs on one side *A. albotaeniatus*
12. Inner shoulder hair with branches nearly as long as the whole hair 13
 Inner shoulder hair simple or with few short branches near the tip 14
13. Outer clypeal hair forming broom-like tuft of 22 to 50 or more branches .. *A. barbirostris*
 Outer clypeal hair with 10 to 20 branches, not forming such a tuft *A. barbumbrosus*
14. Outer clypeal hair with 30 or more thick branches *A. hyrcanus sinensis*,
A. hyrcanus nigerrimus, *A. hyrcanus* subsp. near *sinensis*.
 Outer clypeal hair with not more than fifteen fine branches *A. montanus*
15. Anterior tergal plates on segments II to VII small, not involving the median posterior plates 16
 Anterior tergal plates on segments II to VII very large, involving the median posterior plates *A. fluviatilis*, *A. aconitus*, *A. varuna*, *A. minimus*
16. Outer clypeal hair simple or with short side hairs 17
 Outer clypeal hair with long brush-like branches 26
17. Inner shoulder hair with large darkly pigmented root, the hair tending to stoutness with numerous branches 18
 Inner shoulder hair with small unpigmented or lightly pigmented root, the hair tending to slenderness, or with few branches 22
18. Abdominal palmate hair II fully developed with well differentiated filaments 19
 Abdominal palmate hair II with filamentous branches, lanceolate leaflets, or rarely with poorly differentiated filaments 20
19. One of the long mesothoracic pleural hairs with lateral branches *A. parangensis*
 All long mesothoracic pleural hairs simple *A. hackeri*
20. Outer clypeal hairs with side hairs 21
 Outer clypeal hairs simple, without side hairs *A. leucosphyrus balabacensis*,
A. leucosphyrus pujutensis.
21. Lateral hair on abdominal segment V with two to six branches; filaments of abdominal palmate hairs with fine sharp tips (when undamaged) *A. maculatus*
 Lateral hair on abdominal segment V with 6 to 14 branches; filaments of abdominal palmate hairs with blunt tips *A. karwari*
22. Outer clypeal hair half, or less than half, the length of inner; one long hair of metathoracic pleural group much more sparsely branched than the other 23
 Outer clypeal hair half or more the length of inner; long hairs of metathoracic pleural group simple or branched to about the same degree 24
23. Posterior clypeal hairs placed approximately in line with inner clypeal hairs and some distance from them *A. vagus limosus*
 Posterior clypeal hairs placed close to and internal to inner clypeal hairs .. *A. vagus vagus*
24. Abdominal palmate hairs with poorly differentiated filaments, not more than one-third the length of the blades 25
 Abdominal palmate hairs with sharply differentiated filaments, nearly as long as the blade ... *A. sundaticus*, *A. litoralis*, *A. budlowi*, *A. subpictus subpictus*, *A. subpictus malayensis*
25. Abdominal palmate hairs I and II with lanceolate leaflets; antennae and clypeal hairs lightly pigmented *A. kochi*
 Abdominal palmate hairs I and II with branches filamentous or slightly flattened; antennae and clypeal hairs deeply pigmented *A. tessellatus*
26. Posterior clypeal and trans-sutural hairs with two to nine branches from near bases .. 27
 Posterior clypeal and trans-sutural hairs simple or forked distally *A. annularis*,
A. schuffneri.
27. Abdominal palmate hairs with filaments less than half the length of the blade; shoulder hairs with lightly pigmented roots *A. philippinensis*
 Abdominal palmate hairs with filaments at least half the length of the blade; shoulder hairs with deeply pigmented roots *A. pallidus*

DESCRIPTION OF SPECIES.

A. (A.) AITKENII AITKENII James.

JAMES. S. P., in THEOBALD, F. V., 1903.—Mono. Culic., 3: p. 22.

Type locality: Karwar, W. India.

Specimens examined: Six larvae.

Larva.

Head (Fig. 1a): ic. usually bifid, about one-third length from base, may be trifid or simple; short side hairs present in region of fork; oc. about one-third length of ic., simple or bifid at tip; pc. shorter than oc., with 3-4 branches from near base; sut. and t. sut. with 3-6 branches; antennal hair 7-10 branched, approx. equal in length to oc.; frontal hairs extending past anterior margin of head.

Shoulder hairs (Fig. 1b): is. short, with 8-11 branches radiating from a short, stout, flattened stem, root inconspicuous; cs. longer, 10-17 branched, with stout stem and prominent root. Pleural hairs; ppl. with 2 long simple, 1 medium 3-6 branched, and 1 short 2-4 branched; mpl. with 2 long, 1 short, and 1 minute, all simple; mtpl. with 1 long simple, 1 long 3-4 branched, 1 short 2-4 branched, and 1 minute simple. Mt. palm. developed, with lightly pigmented, lanceolate leaflets.

Abdominal palmate hairs (Fig. 1c): abd. I developed, with narrow, unpigmented, lanceolate leaflets; abd. II with lanceolate or poorly differentiated leaflets; abd. III-VIII fully developed, filaments with broad base and sharp tip, one-fourth to one-third of the blade, pigment rather light, even. Saddle hair with 3-6 branches.

Biology.

Larvae of this species were found only in well-shaded, fresh, clean water in seepages, jungle pools, etc. Adults were never taken in the field, and, due to difficulty experienced in breeding through larvae in the laboratory, no adult specimens were obtained for examination.

Notes.

The larvae are readily identified by their small size and characteristic clypeal hairs. The specimens described above appear to conform with the "Malayan type" of Gater (1934), but differ in the quite frequently trifid inner clypeal hairs. In this they resemble the Philippine form tentatively identified as *A. aitkenii bengalensis* by Russell, and Baisas (1934).

These larvae probably represent a local form, allied, or identical with that of the Philippines.

Distribution.—Brunei: Brooketon, Brunei; Brit. North Borneo: Beaufort.

A. (A.) BREVIPALPIS ROPER.

ROPER, R., 1914.—*Bull. Ent. Res.*, 5: p. 137.

Type locality: Membakut, Brit. North Borneo.

Specimens examined: Four females, two males, sixteen larvae.

Female.

Labium (Fig. 2b) smooth, brown; palps (Fig. 2b) brown, thin, shaggy near base, three-fourths to seven-eighths the length of the proboscis. Antennae with dark scales on seg. 3. Head scales numerous; vertical pale spot small and indistinct; interocular vertex very narrow.

Mesonotum brown, hairy; a few narrow scales at centre of anterior margin. Pn. I. with dark scales on anterior face. Pleura brown, shiny; pr. s. 2-4; ust. s. 2-5; 1st s. 2-4; sp. s. 2-3.

Wing (Fig. 2a) concolorous; first fork cell much longer than second; cross-vein 2-3 distal to 3-4, 4-5 proximal to both.

Legs uniformly brown, unornamented; coxae without scales.

Abdomen and cerci entirely without scales.

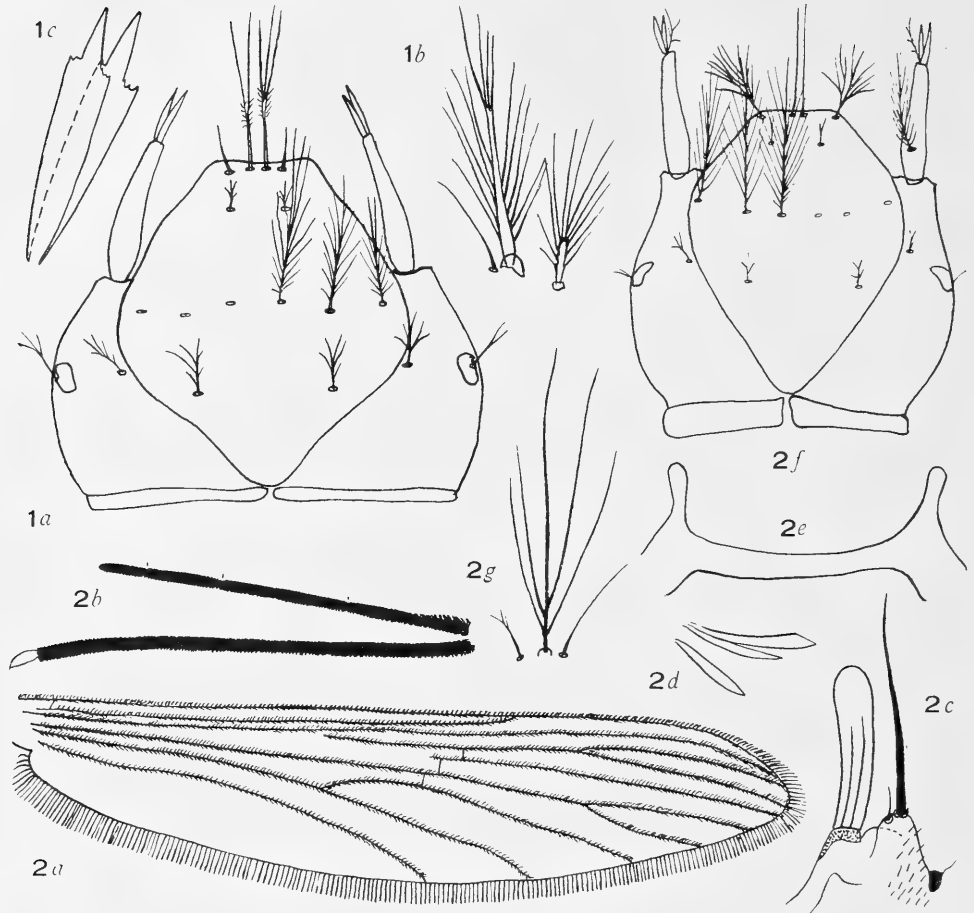
Male.

Generally similar to the female; antennae without scales; palps as long as or longer than the proboscis; wing sparsely scaled.

Terminalia: Coxites unscaled; phallosome rather short, each side with 3-4 scimitar-shaped leaflets, and sometimes another, short and spine-like (Fig. 2d). Harpago (Fig. 2c) with rather narrow, curved club; ventral lobe very prominent with strong apical spine, a little longer than club, and a very short seta external to it. A small chitinous plate present at the V-shaped junction of the harpagones. Processes of the 9th tergite rather short, equal to about one-half the distance between them (Fig. 2e).

Larva.

Head (Fig. 2f): ic. long, simple or 2-3 branched toward the tip; oc. almost as long as ic. with 7-12 more or less dichotomous branches; pc. long, reaching the base of ic., simple or bifid, rarely trifid, at one-third or more the distance from the base; sut.



Text-figures 1 and 2.

Fig. 1.—*A. aitkenii aitkenii* James. (a) Larval head $\times 205$. (b) Shoulder hairs $\times 570$. (c) Leaflets from abdominal palmate iv $\times 190$.

Fig. 2.—*A. brevivalpis* Roper. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Leaflets of phallosome $\times 910$. (e) Male 9th tergite $\times 420$. (f) Larval head $\times 120$. (g) Shoulder hairs $\times 205$.

longer than pc., 1-3 branched, t. sut. long, 2-6 branched; antennal hair with 12-15 branches, placed about one-third distance along the shaft.

Shoulder hairs (Fig. 2g): is. simple or with 2-3 branches towards the tip; cs. with 3-7 branches, usually from near the base. Pleural hairs: ppl. with 3 long simple, 1 very short, stout, brush-like, with 4-12 branches; mpl. with 2 long simple, 1 short simple or 2-4 branched, and 1 minute simple; mtpl. with 2 long simple (1 noticeably longer and stouter than the other), 1 short simple or 2-3 branched, 1 very short simple, rarely bifid. Mt. palm. undeveloped, with filamentous branches. Mesothoracic hair no. 1 weak, with 6-10 fine branches.

Abdominal palmate hairs undeveloped, with filamentous branches only.

Abdominal hair no. 0 present, 2-3 branched, but extremely small. Lateral hair on abd. IV with 2-4 branches at about one-half way from base, that on abd. V, 1-3 branched near base, and that on VI with 3-6 branches, radiating from near base. Psp. 2-4 branched.

Biology.

Larvae of this species were probably the most common of the jungle breeding forms in the Kuala Belait area, usually occurring amongst rotting leaves in the peaty water of

jungle pools. There seemed to be a preference for the more open but still well-shaded situations, nearer to the jungle fringe and along tracks.

The adults were never taken in the field, but Roper (1914) records this species as entering houses in fair numbers. His dissections were all negative, however, and there is no evidence to indicate it as a possible vector species.

Notes.

Apart from the very small *A. aitkenii*, this is the only species of the series *Anopheles* known to occur in the area, and is readily distinguished by the large size and the complete lack of white ornamentation on palps, legs or wings. The short palps distinguish it from most other Oriental species in this series.

The larvae are very similar to those of Sp. *A. nr. umbrosus*, and in some specimens are differentiated only with great difficulty. In most specimens, however, the greater number of branches to the outer clypeal hairs, and the longer more distally branched posterior clypeals, give a reasonably certain identification of *brevipalpis*. The form of the central shoulder hair is also of use; in *brevipalpis* the branches are usually long and rise from near the base, while in sp. *A. nr. umbrosus* they tend to rise successively from a definite stem. This character is, however, variable and of confirmatory value only.

The adult material examined showed little difference from Malayan and N.E.I. descriptions, except in the male terminalia, which differ slightly from those described by Swellengrebel and Rodenwaldt (1932). Two specimens showed a small seta on the ventral lobe of the harpago, additional to the apical spine described by the latter authors. The shape of the 9th tergite also differs from that figured by them, but this appears to be due to distortion in the preparation from which their illustration was made.

Larval specimens, including topotypical material from the type locality, showed some variation from Malayan descriptions, principally in the form of the posterior clypeal hairs. In Borneo specimens this hair is simple or 2-3 branched, never 4-7 branched as in Malaya. This creates the above-mentioned difficulty in identification.

As noted by Gater (1933a), the larval description from Strickland and Chowdhury, quoted by Swellengrebel and Rodenwaldt (op. cit.), obviously refers to an immature instar.

Distribution.—Brunei: Kuala Bekait; Sarawak: Miri (Stokes); Br. Nth. Borneo: Kimanis, Membakut (Roper).

A. (A.) ALBOTAENIATUS Theobald.

THEOBALD, F. V., 1903.—Mono. Culic., 3: p. 88.

Type locality: Perak, Federated Malay States.

Specimens examined: Three females, one male, five larvae.

Female.

Labium (Fig. 4b) dark, shaggy ventrally; palps (Fig. 4b) shaggy, dark or with an inconspicuous basal pale band on segment 5. Clypeus bare. Antenna with dark scales on segments 2 and 3. Vertical pale spot very small.

Mesonotum dark with longitudinal lines; anterior margin with central tuft of dark scales and rather prominent lateral tufts of mixed pale and bronzy scales. Pleura dark. Pn. I. with dark scales. Pr. s. 2-4; ust. s. 2-5; l. st. s. 4-5; sp. s. 2, fine.

Wing (Fig. 4a): Costa dark with small subcostal and apical pale spots, the latter involving the tip of vein 1; the former may also partially involve vein 1. Vein 1 dark with scattered pale scales basally, and small pale spots in the sector, accessory sector and apical regions. Vein 2 dark; 2-1 dark with a small subapical pale spot; 2-2 with a pale spot towards the base. Vein 3 dark at base, remainder pale or with some mixed scaling. Vein 4 dark with a few scattered pale scales; 4-1 and 4-2 dark basally, remainder mixed pale and dark. Vein 5 with sub-basal dark spot, remainder mixed pale and dark; 5-1 largely pale, with dark spot at m-cu and apex, and a few dark scales or a dark spot between them; 5-2 dark on apical half, remainder pale or with a few dark scales. Vein 6 pale with prominent central dark spot and some dark scales at base and apex. Remigium dark, pale at centre. Humeral cross-vein dark scaled. Fringe pale between 2-2 and 3.

Legs: Coxae without scales. Fore and mid-femora dark, hind minutely pale at apex. Fore-tibia pale at apex, mid- with small basal and minute apical pale bands, hind pale at base and apex, the latter quite prominent. Fore-tarsi with small incomplete apical pale bands on segs. 1 and 2 and a faint band on seg. 3; mid-tarsi dark, or with a faint indication of banding on segs. 2 and 3; hind tarsi with small basal and apical bands on seg. 1, a wider apical band on seg. 2, segs. 3 and 4 largely white, with a central dark band equal to about one-third of the segment; seg. 5 pale.

Abdomen without scales.

Male.

Generally similar to female. Palps dark with a few pale scales at base of club. Wing extensively pale. Pale apical band on hind tibia very small.

Terminalia: Phallosome with three pairs of long, subequal leaflets, the largest with fine serrations on the inner margin. Harpago (Fig. 4c) with prominent ventral lobe bearing a stout apical spine, longer than the club, and a much shorter external hair beside it. Processes of the 9th tergite long and thin, in length about three-fourths of the distance between them (Fig. 4d).

Larva.

Head (Fig. 4e): ic. simple, placed wide apart, the distance between them approximately equal to that between ic. and oc.; oc. with 17-27 long fine branches; pc. short, fine 2-3 branched; sut. 3-4 branched; t. sut. 4-6 branched.

Shoulder hairs (Fig. 4f): is. simple or bifid; cs. 5-8 branched; both with inconspicuous roots. Pleural hairs: ppl. with 3 long simple, 1 very short, 2-4 branched; mpl. with 2 long, 1 short, and 1 very short, all simple; mtpl. with 2 long and 1 minute, both simple, and 1 short simple or bifid. Mesothoracic hair no. 1 with small stem and 13-21 branches. Mt. palm. developed with clear lanceolate leaflets.

Abdominal palmate hairs (Fig. 4g): abd. I and II developed with clear lanceolate leaflets; abd. III to VII developed, leaflets poorly differentiated, but strongly serrate on the distal one-third; dense, uneven pigment on the basal two-thirds. Lateral hairs on abd. IV and V simple.

Biology.

This species was of rare occurrence, but larvae were occasionally found in heavily shaded jungle pools of peaty water, associated with *A. brevipalpis* and *A. umbrosus*; a few larvae were also taken in a more open situation on the fringe of a sago swamp. Several adults were taken biting man in the open during early evening; one was dissected but gut and gland were negative. There is no evidence that this species plays any part in malaria transmission.

Notes.

The adult of this species is easily recognized, even with the naked eye, by the conspicuously white hind tarsi, and absence of a ventral scale tuft. The larva also is easily identified by the widely spaced inner clypeal hairs.

The few specimens examined were typical of the species as described by Gater (1935), but none showed the pale ring at the apex of the labium figured by Swellengrebel and Rodenwaldt (1932). The male harpago also differed from that described by the latter authors, in possessing a short external spine on the ventral lobe.

Distribution.—Brunei: Kuala Belait; Sarawak: Miri (Stokes); Br. Nth. Borneo: Papar; Membakut (Roper).

A. (A.) BARBIROSTRIS van der Wulp.

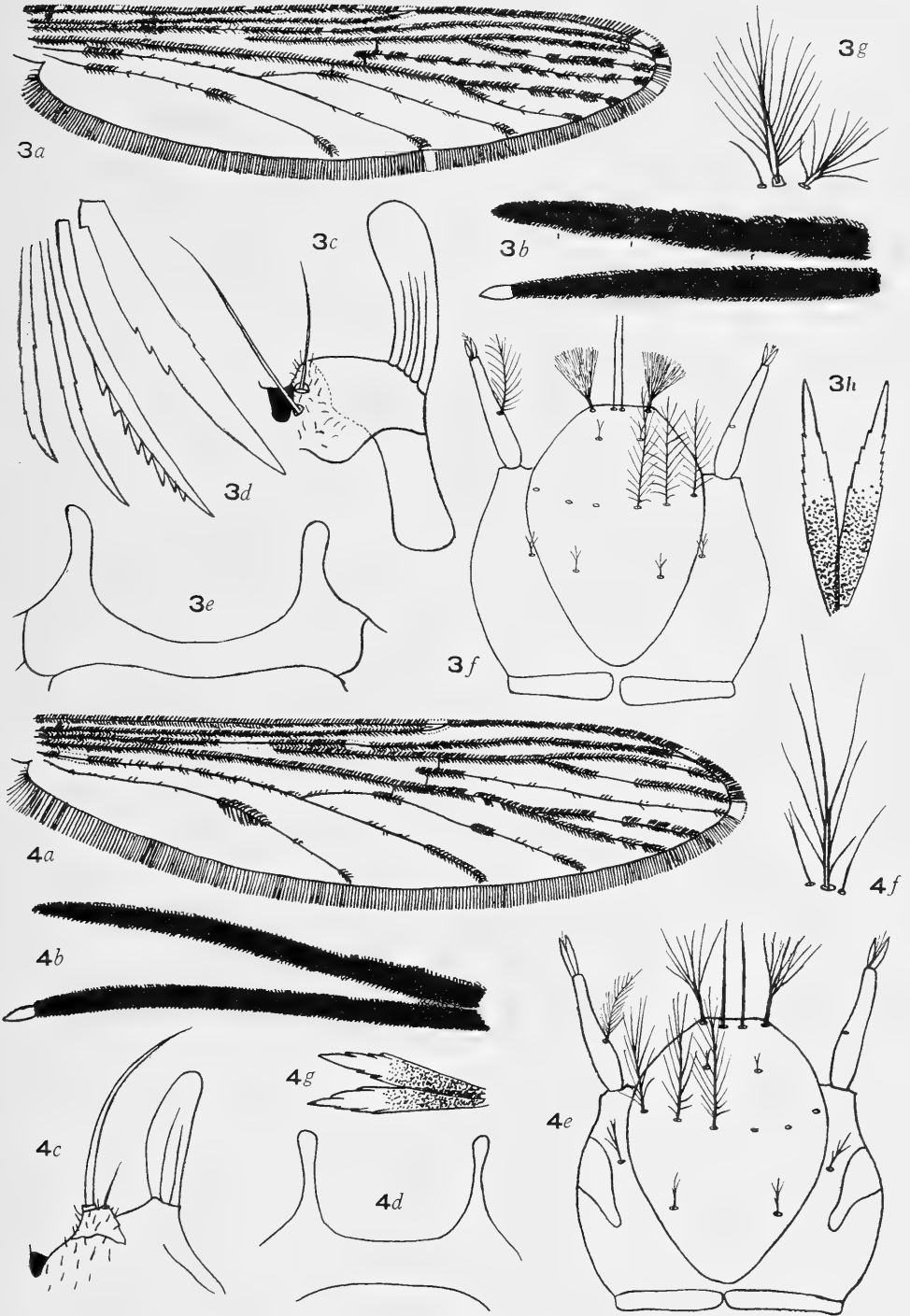
VAN DER WULP, 1884.—*Notes from the Leyden Museum*, 6: p. 248.

Type locality: Mt. Ardjoeno, East Java.

Specimens examined: Twenty-five females, four males, numerous larvae.

Female.

Labium (Fig. 3b) dark, very shaggy. Palps (Fig. 3b) dark, very shaggy. Clypeus bare. Antenna with numerous dark scales on seg. 2, a dark tuft on seg. 3. Vertical pale spot small.



Text-figures 3 and 4.

Fig. 3.—*A. barbirostris* van der Wulp. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Leaflets of phallosome $\times 910$. (e) Male 9th tergite $\times 420$. (f) Larval head $\times 120$. (g) Shoulder hairs $\times 205$. (h) Leaflets from abdominal palmate iv $\times 570$.

Fig. 4.—*A. albotaeniatus* Theobald. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Male 9th tergite $\times 420$. (e) Larval head $\times 120$. (f) Shoulder hairs $\times 205$. (g) Leaflets from abdominal palmate iv $\times 570$.

Mesonotum dark, somewhat paler on the median area; anterior margin with central tuft of narrow pale scales, lateral tufts of broader scales. Pn. 1 with prominent dark tufts. Pleura dark. Pr. s. 3-5; ust. s. 3-6; sp. s. 5-10; variable patches of pale scales usually accompanying hairs on propleuron, sternopleuron and mesepimeron.

Wing (Fig. 3a): Costa speckled on basal one-half with pale scales of varying extent, from a few single scales to groups forming small pale spots; subcostal spots small, variable; apical pale spot involving apex of vein 1. Vein 1 with prominent sector pale spot and variable pale speckling towards the base and from the accessory sector region to past the subcostal region. Vein 2 dark; 2-1 dark with pale apical spot; 2-2 mainly dark with a pale sub-basal spot and variable pale speckling. Vein 3 with dark basal and apical spots, mixed pale and dark scales between. Vein 4 dark; 4-1 and 4-2 dark at base and apex, pale or mixed between. Vein 5 with dark sub-basal spot, remainder speckled; 5-1 with dark spots at base and apex and at cross vein m-cu., remainder speckled; 5-2 dark apically. Vein 6 speckled on basal one-half, dark at apex and centre. Remigium dark with pale central spot at anterior and posterior margins. Fringe pale at apices of veins 2-1, 3 and usually 5-2.

Legs: Femora with pale band at base and often at apex. Tibiae pale at apex and often at base. Some pale scaling on under surface of mid- and hind femora. Fore tarsi with apical pale bands on segs. 1 and 2; mid-tarsi with very narrow pale apical banding on segs. I-IV, these sometimes faint or absent; hind tarsi with narrow apical bands on segs. I-IV, and a narrow basal band on V. Coxae usually with tufts of pale scales on all legs.

Abdomen: Dorsal surface without scales. Ventral surface of segs. III-VI (sometimes seg. II) with small but distinct central tufts of pale scales and some scattered dark scales; seg. VII with small pale median tuft on anterior half, followed by a prominent dark tuft on the posterior margin.

Male.

Generally similar to the female. Antenna without scales. Wing without terminal dark spots on vein 6. No ventral tuft on abd. VII, but dorsal surface with a patch of white scales. Club of palp, viewed in certain lights, shows pale bands at base and centre.

Terminalia: Phallosome long with 4-6 pairs of leaflets, half or more strongly serrate on one or both edges; the two largest considerably broader than the others, with a strong tooth at the base (Fig. 3d). Harpago (Fig. 3c) with normal club, and two bristles on the ventral lobe, one longer than the club and one shorter. Some specimens with an additional small bristle on the dorsal face of the harpago. Ninth tergite (Fig. 3e) with clubbed processes, a little more than one-half as long as the distance between them.

Larva.

Head (Fig. 3f): ic. simple; oc. with a large number of branches in a broom-like tuft; pc. bifid or rarely simple; sut. 6-9 branched; t. sut. 5-8 branched. Antennal hair 7-11 branched, placed about the middle of the shaft.

Shoulder hairs (Fig. 3g): is. with 5-10 branches from near base; cs. 12-15 branched, with a fairly prominent root. Pleural hairs: ppl. with 3 long simple, 1 very short with 2-6 spiny branches; mpl. with 2 long, 1 short, and 1 very short, all simple; mtpl. with 2 long simple, 1 short 2-3 branched, 1 minute simple or bifid. Mt. palm. weakly developed with clear lanceolate leaflets. Mesothoracic hair no. 1 with stout flattened stem and 22-25 branches.

Abdominal palmate hairs (fig. 3h): Abd. 1 weakly developed with lanceolate leaflets; abd. II-VII fully developed with long, pointed, poorly differentiated filaments; pigmentation heavy, extending to base of filaments. Lateral hairs on abd. IV and V usually bifid.

Biology.

Larvae of this species were extremely common, occurring in almost any collection of ground water containing vegetation and not subject to extremes of light or shade.

No larvae were found in jungle pools or open water without vegetation, the most favoured situations being padi fields, overgrown drains and open, sedgy swamp.

Adults were taken biting man in the open and in houses during early evening, and inside the jungle during daylight; however, they appeared to be more frequent in the vicinity of cattle. Engorged females were found in lighted tents near tethered cattle, apparently attracted to the light after feeding; none could be taken with human bait during the same period, and apparently the cattle were a more attractive bait. Unfed females were also attracted to light occasionally, but made no attempt to feed on humans present.

Dissection of eight specimens showed all with negative glands, but of five guts examined, one was positive, containing several small sporocysts. While it seems unlikely that this species is a vector of major importance, due to its zoophilic feeding habits, its potentialities should not be overlooked, since it will feed on man, and is a local vector of some importance in Malaya and Celebes.

Notes.

The species is readily distinguished from most others present in the area by the very shaggy, dark palps, the banded tarsi, and the pale scales on the basal one-third of the costa. The larva is very similar to that of *A. hyrcanus*, but is distinct in the branching of the inner shoulder hair. *A. barbumbrosus*, which also occurs in Nth. Borneo, is very similar to *barbirostris*, but lacks the scaling on the venter of the abdomen and has simple leaflets on the male phallosome; the larva has fewer branches to the outer clypeal hairs (11-22 according to Christophers (1933)).

The Borneo form agrees fairly well with the forms described from other areas, with the exception of the Philippines. According to Russell and Baisas (1936), in the latter country white scaling on the venter is very rare; in the Borneo form, this character is quite conspicuous, in some specimens even more so than in the Philippine *A. pseudo-barbirostris*.

The literature dealing with this species shows quite a considerable amount of local variation in morphology and physiology, and division into a series of subspecies or races should be possible. That this may be of use is shown by the two Malayan forms (Reid 1941), of which one is a vector and the other apparently harmless.

Distribution.—Brunei: Brooketon, Brunei, Limbang, Kilanis, Kuala Belait (local report); Sarawak: Lutong, Miri; Br. Nth. Borneo: Beaufort, Papar, Jesselton, Membakut (Roper).

A. (A.) BARBUMBROSUS Strickland and Chowdhury.

STRICKLAND, C., and CHOWDHURY, K. L., 1927.—*Illust. Key Anoph. Larvae of India*, p. 18.
Type locality: Noesa, Java, or Mandailing, Sumatra.

Specimens examined: One larva.

Only one specimen of this species, a 4th instar larva, was taken; no description is therefore given, but the above specimen conformed with the description given by Gater (1934).

Distribution.—Brunei: Kuala Belait (local report); Labuan Is.

A. (A.) HYRCANUS NIGERRIMUS Giles.

GILES, G. M., 1900.—*Handbook of Gnats or Mosquitoes*. 1st Ed., p. 161.

Type locality: Calcutta, India.

Specimens examined: Thirty-two females, eleven larvae.

Female.

Labium (Fig. 5*b*) dark, rather shaggy. Palps (Fig. 5*b*) shaggy; seg. 5 all white or with some dark scales at centre; narrow pale bands at junction of segs. 2-3, 3-4, and 4-5, and a central patch of pale scales on inner side of seg. 2; remainder of palp dark, usually with liberal admixture of pale scales. Clypeus with lateral tufts of broad dark scales. Vertical pale spot small, with mixed forked and hair-like scales. Antenna with broad scales on segs. 2 and 3, and a few scattered on other segments up to seg. 9. Mesonotum dark grey with darker longitudinal lines; anterior margin with central tuft of fine pale scales, and lateral tufts of narrow pale scales above, and broad dark ones below. Pn. 1. with prominent dark tufts. Pleura dark with grey areas, unscaled. Pr. s. 3-5; ust. s. 3-4; l. st. s. 4-6; sp. s. 2-3.

Wing (Fig. 5a): Costa dark, except for rather small subcostal, and prominent subapical pale spots, the former usually not involving vein 1; the latter does not extend along the costa as far as the apex of vein 1. Vein 1 with prominent sector and subapical pale spots, and liberal sprinkling of pale scales along almost its entire length. Vein 2 dark, with some mixed scaling distally; 2-1 with a subapical pale spot; 2-2 with a pale spot near the centre and some mixed scales. Vein 3 with apical and basal dark spots and a variable amount of dark scaling between. Vein 4 mainly dark with a variable admixture of pale scales on the distal one-fourth; 4-1 and 4-2 dark apically and basally. Vein 5 with long dark spot near base, remainder pale; 5-1 with dark spots at apex and m-cu cross-vein, variable amount of dark scaling between, and a few dark scales at base; 5-2 dark apically. Vein 6 with central and apical dark spots. Humeral cross-vein unscaled. Fringe pale from apex of vein 1 to between 3 and 4-1, and rarely at apex of 5-2.

Legs: Mid coxa with patches of pale scales; occasionally a few on fore and hind coxae. Fore femora pale beneath on the apical third; all tibiae and mid and hind femora entirely pale beneath. Femora and tibiae of mid and hind legs with pale apical bands. Fore tarsi with prominent apical pale bands on segs. 1-3 and occasionally a small one on seg. 4; mid tarsi similar; hind tarsi (Fig. 5c) with prominent apical bands of increasing width on segs. 1-3, seg. 4 pale with central band of dark scales; seg. 5 and sometimes seg. 3 with pale basal band.

Abdomen without scales except for a dark ventral tuft, posteriorly on abd. VII.

Male.

The male is not known.

Larva.

Head (Fig. 5d): ic. simple or bifid at tip; oc. with some 30-50 branches in a broom-like tuft; pc. 2-5 branched; sut. 15-20 branched, t. sut. 9-13 branched, both with strong stem and long branches (fig. 5e). Antennal hair long, many branched, placed about one-third of the distance along shaft.

Shoulder hairs (Fig. 5f): is. 2-4 branched towards tip or bifid near base; cs. 8-15 branched; both with small root. Pleural hairs: ppl. with 3 long simple, 1 very short with 3-6 stout brush-like branches; mpl. with 2 long, 1 short, 1 very short, all simple; mtpl. with 2 long simple, 1 short 2-3 branched, 1 minute simple. Mt. palm. with large, clear, lanceolate leaflets. Mesothoracic hair no. 1 with stout stem, long branches.

Abdominal palmate hairs (Fig. 5g): abd. I and II poorly developed with clear, lanceolate leaflets; abd. III-VII with poorly differentiated leaflets and rather diffuse pigment, more or less confined to the basal two-thirds of the leaflets. Lateral hairs of abd. IV and V bifid near base.

Biology.

Larvae were frequently found amongst vegetation in stagnant pools in the open, particularly in padi fields, and other situations where green algae were plentiful. Heavy breeding was also found amongst thick sedge in swamps in open country.

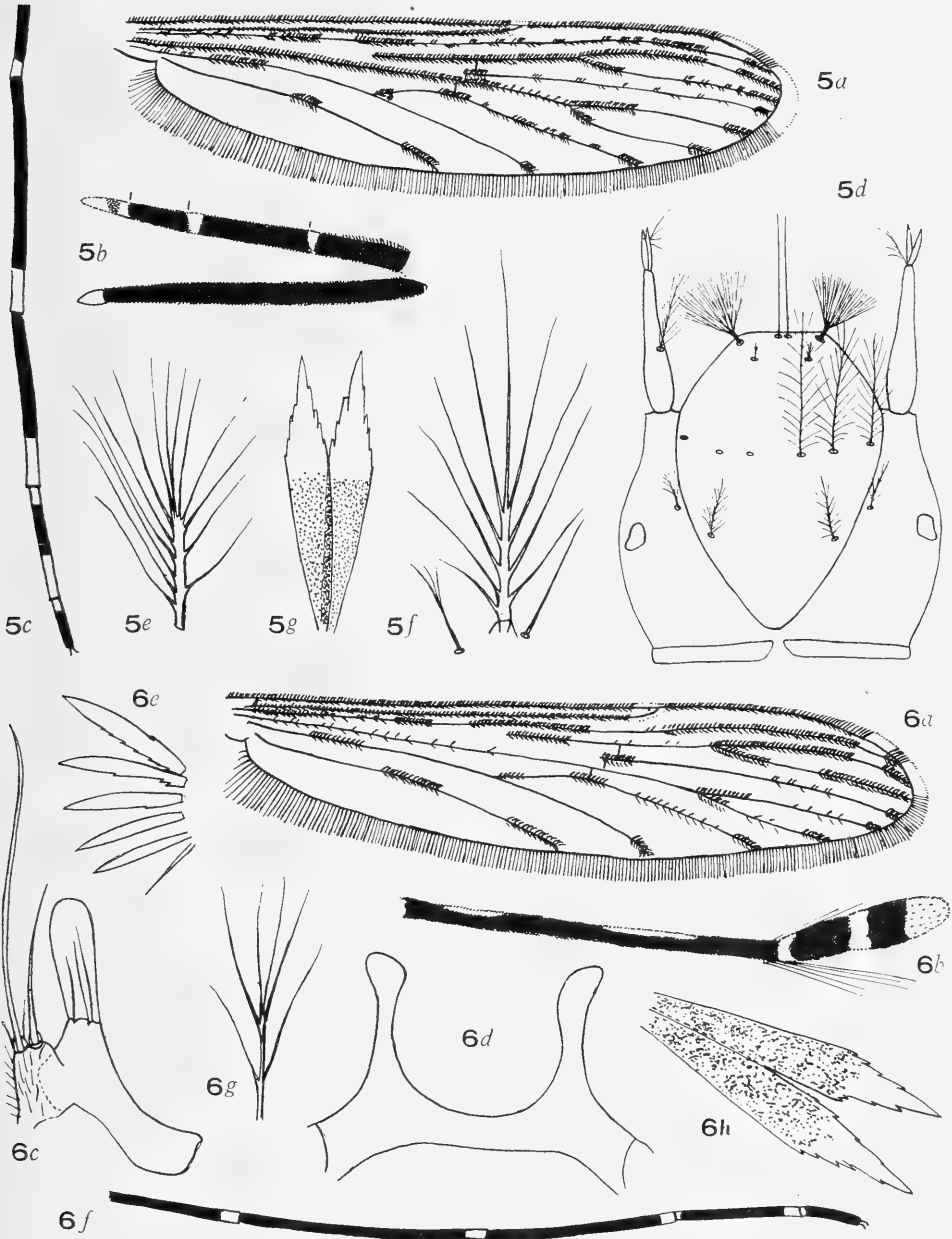
Adults were taken biting, both inside houses and in the open, during the first few hours of darkness, and, though often taken with animal bait, seemed to prefer human blood. Dissections of 69 salivary glands and 61 guts were all negative.

Notes.

The pale bands on the palps distinguish this from most other species of the subgenus *Anopheles* present in the area; other characteristic features are the large apical fringe spot on the wing, and the dark ventral tuft of the abdomen. From the subspecies following, it differs in the smaller subcostal spot, wider apical fringe spot, scaled coxae, and the broad bands on the hind tarsi.

The larva, with its bushy outer clypeal hairs, is similar only to *A. barbirostris*, but is distinct in the form of the inner shoulder hair, which is simple or has short branches at the tip. Subspecific identification is difficult in the larval stage but several tentative characters are given in the description of the next subspecies.

Borneo specimens agree fairly well with descriptions of this subspecies from other parts of the Orient, although many appear to have an abnormal amount of pale scaling on the palps. Most specimens examined showed very few dark scales or none at all on seg. 5, and large pale areas on the dorsum of segs. 2-4. The apical fringe spot of



Text-figures 5 and 6.

Fig. 5.—*A. hyrcanus nigerrimus* Giles. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Hind tarsus $\times 55$. (d) Larval head $\times 120$. (e) Sutural hair $\times 570$. (f) Shoulder hairs $\times 420$. (g) Leaflets from abdominal palmate iv $\times 910$.

Fig. 6.—*A. hyrcanus* subsp. near *sinensis*. (a) Wing $\times 55$. (b) Male palp $\times 55$. (c) Harpago $\times 570$. (d) Male 9th tergite $\times 420$. (e) Leaflets of phallosome $\times 910$. (f) Hind tarsus $\times 55$. (g) Sutural hair $\times 570$. (h) Leaflets from abdominal palmate iv $\times 910$.

the wing also differed from that described from the Philippines; in the latter, this spot commences at the apex of vein 2·1 (Russell and Baisas, 1936), whereas in the Borneo form it commenced at vein 1 or a little before it.

In the larva, the sutural and trans-sutural hairs are rather more strongly branched than usually recorded, but agree well with the "type B" of Swellengrebel and Rodenwaldt (1932).

Scharff (1927), in his survey of Labuan Is., records only *hyrcanus sinensis*; a detailed survey in 1945, however, showed *nigerrimus* prevalent and true *sinensis* absent or extremely rare. Unless the population has undergone a remarkable alteration, it seems that the earlier record actually refers to *nigerrimus*.

Distribution.—Brunei: Brooketon, Kuala Belait (local report); Labuan Is.; Br. Nth. Borneo: Papar, Jesselton.

A. (A.) HYRCANUS subsp., near SINENSIS.

Specimens examined: One female, five males, two larvae.

This subspecies is generally similar to the preceding, but differs in the characters set out below.

Female.

1. General appearance less shaggy.
2. Palpi more distinctly banded, with less scattered pale scaling.
3. Coxae without scales.
4. Wing (Fig. 6a) with subcostal spot involving vein 1 to a greater degree; vein 1 with less scattered pale scaling, confined to the basal one-third and subcostal region; vein 2 largely pale with basal and distal dark spots; vein 4 dark at base, the remainder with mixed scaling; the dark spot at base of vein 5 rather long; apical fringe spot much shorter, extending from the tip of vein 1 only to the tip of vein 2·2 or a little past it.
5. Legs dark, except for small basal and apical bands on mid and hind tibiae. Fore tarsi with small apical bands on segs. 1-3; mid tarsi similar, with minute apical and basal bands on seg. 5; hind tarsi (Fig. 6f) with narrow apical bands on segs 1-4, narrow basal bands on segs. 4 and 5.

Male.

Generally similar to female. Palp as in Fig. 6b. Abdomen without scales except on coxites. Tarsi with less pale scaling on segs. 4 and 5.

Terminalia: Phallosome with 3-6 pairs of blade-like leaflets and several small and spine-like, the largest and sometimes the second largest, with prominent serrations on the inner margin (Fig. 6e); harpago (Fig. 6c) with broad club, strong apical spine, 1·5-2 times the length of the club, and a shorter external spine, a little shorter than the club; one specimen had the apical spine replaced by a short, weak hair, and the external spine absent; 9th tergite (Fig. 6d) with long clubbed processes, about as long as the distance between them.

Larva.

The several specimens examined differed from the preceding subspecies as follows:

1. Sut. 7-8 branched; t. sut. 6-7 branched; both with weak stem and fine branches (Fig. 6g).
2. Abdominal palmate hairs with patchy pigmentation, extending to the base of, or into the filaments (Fig. 6h).

Biology.

Larvae were found in small numbers amongst tall grass or sedge in open swamps; one larva was also recorded breeding with *A. baezi*, in brackish water. The adults were taken biting man at dusk and dawn, but were not frequent. Dissections of nine adults showed no parasites in guts or glands.

Notes.

The form described above, taken in a limited area in southern Brunei, appears to be an undescribed subspecies or species, most closely related to *A. hyrcanus sinensis*

Wiedemann. The less shaggy appearance, larger subcostal spot, and smaller tarsal bands agree with the latter form, but there is a sharp differentiation in the very short apical fringe spot, the absence of scales on the coxae, and the presence of small basal bands on segs. 4 and 5 of the hind tarsi.

Full descriptions of the Philippine subspecies, *pseudosinensis* Baisas (1935) and *lesteri* Baisas and Hu (1936), could not be obtained, but from the brief notes given by Russell, Rozeboom and Stone (1943), the above form does not appear to correspond with either. However, this uncertainty and lack of sufficient specimens make it undesirable for the present to name and describe the above form as a new species or subspecies.

It seems probable that this is the form occurring in Northern Sarawak, referred to as *sinensis* by Stookes (1927), and thought by him to be a vector of malaria in the vicinity of Miri.

Distribution.—Brunei: Kuala Belait.

A. (A.) SEPARATUS Leicester.

LEICESTER, G. F., 1908.—The Culicidae of Malaya, p. 36.

Type locality: Kuala Lumpur, Malaya.

Specimens examined: Thirty-four females, nineteen males, numerous larvae.

Female.

Labium (Fig. 7*b*) dark, shaggy near base. Palpi (Fig. 7*b*) rough with variable ornamentation; seg. 5 usually entirely pale, rarely with apical half dark; seg. 4 dark, with indistinct pale bands at either base or apex, or sometimes at both; segs. 2 and 3 sometimes with pale scales apically. Clypeus bare. Antenna with broad dark scales on seg. 2 and a patch of pale scales on seg. 3. Vertical white spot with long lanceolate scales anteriorly, short forked ones posteriorly.

Mesonotum dark, with blue-grey bloom on median area; anterior margin with central tuft of narrow pale scales and lateral tufts of broader scales. Pn. 1 with dark tufts. Pleura dark with some linear grey areas, unscaled; ppl. s. 2-4; ust. s. 1-3; sp. s. 1-4.

Wing (Fig. 7*a*): Costa dark, except for prominent apical and subcostal pale areas, the latter involving vein 1, the former extending to the tip of vein 1 or a little past it. Vein 1 dark with sector, subcostal, and apical pale areas; occasionally a few pale scales between sector and subcostal spots. Vein 2 dark basally, remainder pale or mixed; 2·1 dark with subapical pale spot; 2·2 pale, dark at base and apex. Vein 3 dark at base and apex, pale between. Vein 4 dark basally for a variable distance, remainder pale or mixed; 4·1 dark at base and apex; 4·2 dark at apex. Vein 5 with long basal dark spot, otherwise pale; 5·1 with dark spots at apex and crossvein m-cu, a few dark scales at base; 5·2 dark apically. Vein 6 with central and apical dark spots. Remigium dark. Apex of wing dark between veins 1 and 2·1; pale fringe spot from between 2·1 and 2·2 to 3.

Legs: Coxae without scales. Femora and tibiae brown, the former somewhat paler beneath; tarsi with narrow apical pale bands on segs. 1-4, smallest on 4; seg. 5 sometimes pale apically.

Abdomen without scales.

Male.

Generally similar to female. Wing with more prominent sector and subcostal pale spots; veins 5·2 and 6 without apical dark spots. Dorsal surface of abd. VIII with numerous narrow pale scales. Palpi dark on segs. 2 and 3, or with a narrow pale area on the latter; club pale with narrow dark median band.

Terminalia: Phallosome strongly curved; each side with 4 large, strongly serrated leaflets and several small and spine-like. Harpago (Fig. 7*c*) apparently trilobed; dorsal lobe with club; ventral lobe with long apical spine, flattened on the distal half, and a shorter external spine, about 1·5 times as long as the club; between them is another very short seta. Processes of 9th tergite short, clubbed, about half as long as the distance between them (Fig. 7*d*).

Larva.

Head: ic. long, simple; oc. long with 7-16 dichotomous branches; pc. short, simple (rarely bifid on one side); sut. 2-5 branched; t. sut. 4-8 branched. Antennal hair placed about one-third distance along shaft, many branched.

Shoulder hairs (Fig. 7e): is. short, with 2-5 branches at the tip, rarely simple; cs. 10-14 branched. Pleural hairs; ppl. with 3 long simple, 1 very short with 2-6 stout branches; mpl. with 2 long simple, 1 short with 2-3 branches, occasionally simple, and 1 minute simple; mtpl. with 2 long simple, 1 short 2-4 branched, and 1 minute simple. Mt. palm. undeveloped, small, with 4-6 branches. Mesothoracic hair no. 1 rather weak.

Abdominal palmate hairs undeveloped, with filamentous branches. Lateral hair of abd. IV with 2-5 branches (rarely up to 7). Psp. 3 branched.

Biology.

Larvae of this species were very common amongst tall sedge and grass in open swamps away from the jungle; it was rarely taken amongst low or open vegetation, and seemed to show a strong preference for the more heavily shaded situations. Despite this preference, no breeding was found in jungle pools, though it occasionally occurred along the jungle fringe. The adult was extremely common in most areas, and was by far the most prevalent Anopheline taken in night catches with human bait. In the Brooketon and Kuala Belait areas, where animals were scarce, biting rates of up to 30 per man per hour were recorded. However, on Labuan Is. and at Jesselton, where cattle were numerous, their blood seemed to be preferred. In the latter area, numerous engorged females were found entering lighted tents, apparently after feeding on cattle, and during this period none at all could be taken with human bait.

Dissections of 254 specimens showed no parasites in the salivary glands, and 200 guts examined were also negative. It appears that this species plays no part or a very minor one in malaria transmission, despite its large numbers and readiness to take human blood.

Notes.

The main characters by which this species is identified are set out in the table on page 93; in most specimens, the general brown colouration and prominent subcostal spot are quite distinctive to the naked eye. Some larval specimens resemble rather closely those of sp. *A.* near *umbrosus* and *brevipalpis*, but the simple posterior clypeals and larger number of branches to the outer clypeals and central shoulder hair usually make identification relatively simple.

All specimens agreed well with descriptions and specimens from Malaya and N.E.I., though one specimen from Jesselton showed an unusual variation in having dark scales on the apical half of palp seg. 5. A larval specimen also showed an unusually large number of branches to the lateral hair on abdominal seg. IV, being 7 branched and thus overlapping the range of *A. baezi gateri*.

Distribution.—Brunei: Brooketon, Brunei, Limbang, Kuala Belait; Sarawak: Miri (Stookes); Labuan Is.; Br. Nth. Borneo: Jesselton, Papar, Membakut (Roper).

A. (A.) BAEZI GATERI (Baisas).

BAISAS, F. E., 1936.—*Philipp. J. Sci.*, 59, No. 1: 65. (*A. gateri*.)

Type locality: Iwahig, Palawan, Phil. Is.

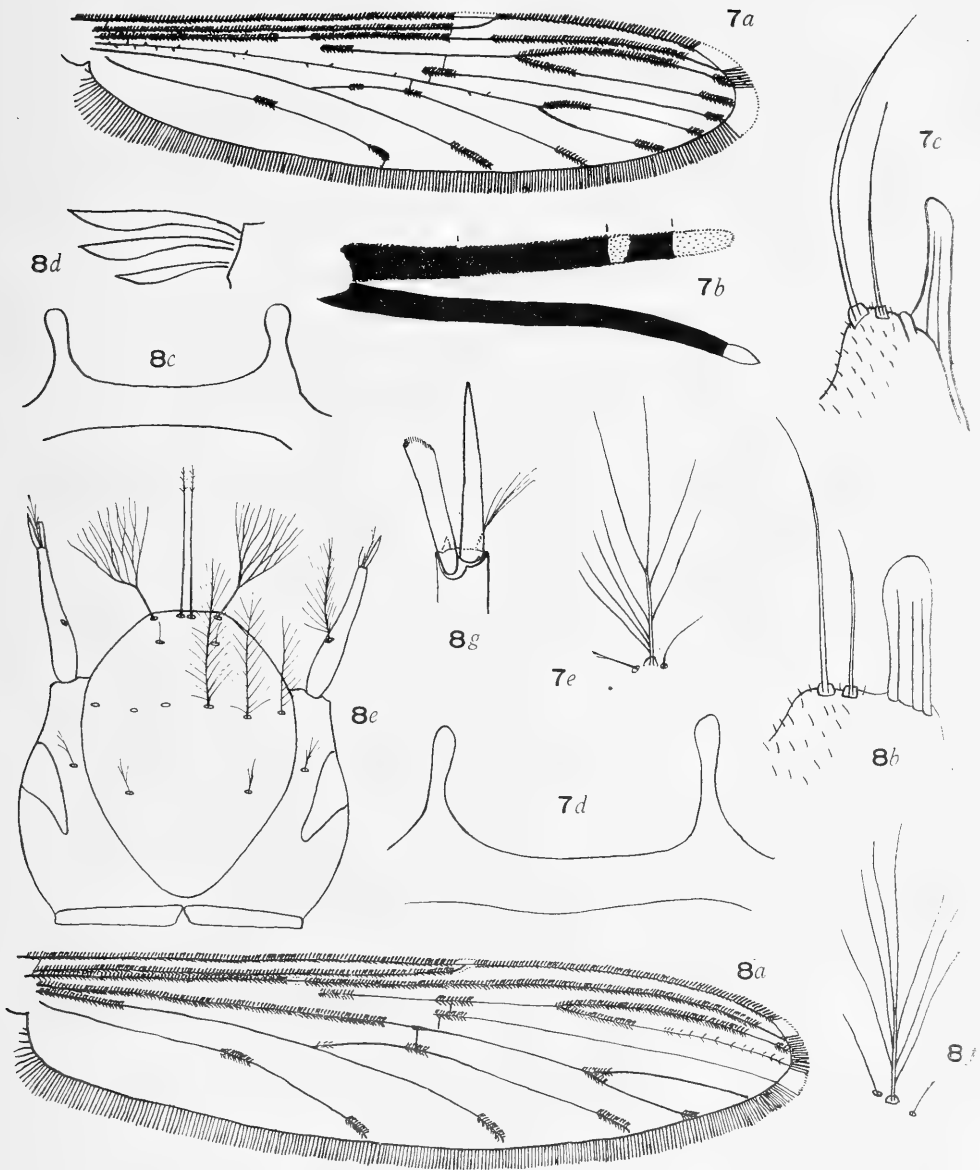
Specimens examined: Twenty-seven females, twenty-one males, numerous larvae.

Female.

Labium dark, rather shaggy. Palpi dark, shaggy. Clypeus bare. Antennae with dark scales on segs. 2 and 3. Vertex narrow; vertical pale spot small, with prominent central bare area, the pale scales longest at the anterior margin.

Mesonotum dark with blue-grey bloom medianly; anterior margin with median tuft of very narrow pale scales and dark lateral tufts behind the pronotal lobes. Pn. 1 with tufts of broad dark scales. Pleura dark with some grey areas; pr. s. 2-4; ust. s. 2-7; upper mesepimeron with variable number, usually small, of flat, dark scales.

Wing (Fig. 8a): Costa dark, except for subcostal and apical pale areas; the latter extending only to the apex of vein 1. Vein 1 dark, with sector and apical pale areas.



Text-figures 7 and 8.

Fig. 7.—*A. separatus* Leicester. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Male 9th tergite $\times 590$. (e) Shoulder hair $\times 205$.

Fig. 8.—*A. baезi gateri* Baisas. (a) Wing $\times 55$. (b) Harpago $\times 570$. (c) Male 9th tergite $\times 420$. (d) Leaflets of phallosome $\times 910$. (e) Larval head $\times 120$. (f) Shoulder hairs $\times 205$. (g) Tip of larval antenna $\times 420$.

Otherwise similar to *A. umbrosus* (p. 91). The sector pale spot on vein 1 and the subcostal spot are variable, the former being absent on 20% of specimens, the latter on 30%, both absent on 10%; on other specimens, either may be represented by a few pale scales only.

Legs: Coxae without scales. Femora and tibiae very dark; mid and hind femora somewhat paler on under surface, hind tibia with a minute pale band. Tarsi uniformly dark, or occasionally with indefinite, minute, pale bands at the joints.

Abdomen devoid of scales.

Male.

Generally similar to female. Antenna without scales. Wing with subcostal spot and sector pale spot on vein 1 usually present and rather larger than on the female; no apical dark spots on veins 5-2 and 6.

Terminalia: Coxites with scales. Phallosome with 3-5 pairs of blade-like leaflets, curved in a somewhat "S"-shaped fashion, occasionally with a few small serrations (Fig. 8*d*). Harpago (Fig. 8*b*) with club on the dorsal lobe, ventral lobe variable; latter usually with strong apical spine and shorter external spine, a little longer than the club; in some specimens these spines may be duplicated on one side, in others the external spine may be shorter than the club or absent. Processes of the 9th tergite rather short and stout, about half as long as the distance between them (Fig. 8*c*).

Larva.

Head (Fig. 8*e*): ic. long with finely frayed tips; oc. with 12-18 dichotomous branches; pc. simple or rarely bifid on one side; sut. 2-4 branched or rarely simple; t. sut. 2-4 branched. Antennal hair many-branched (about 20), situated about one-third of the distance along the shaft. Antenna with one sabre-shaped piece normal, the other short and notched at the tip (Fig. 8*g*).

Shoulder hairs (Fig. 8*f*): is. short, 2-5 branched towards the tip; cs. with 7-9 long branches; os. simple, longer than is. Pleural hairs: ppl. with 3 long simple, 1 very short, 3-6 branched; mpl. with 2 long, 1 short, and 1 minute, all simple; mtpl. with 2 long simple, 1 short, 2-3 branched, 1 minute simple or rarely bifid. Mt. palm. undeveloped, with 4-8 filamentous branches. Mesothoracic hair no. 1 with stout flattened stem and 18-25 branches. Abdominal palmate hairs undeveloped on any segment. Lateral hair of abd. IV with 6-12 branches. Psp. usually 4-6 branched, rarely trifold.

Biology.

Larvae were found in brackish waters, under medium to deep shade, in such situations as overgrown tidal drains, Nipah palm swamp fringes, etc. Salinities recorded ranged from 300 to 1020 parts per 100,000 of chlorine. The adults were not taken in the field.

Notes.

This species is readily identified in the adult stage by the total absence of pale markings on the palps and tarsi, and the general dark appearance. The larva, though rather similar to others in the *umbrosus* group, is differentiated by the 6-12 branched lateral hair of abdominal segment IV, and the notched antennal sabre. Subspecific determination is only possible in the adult stage, on the characters listed in Table 1.

The specimens here described agree very closely with *A. gateri* Baisas, as described by Russell and Baisas (1934 and 1936), but show a degree of variation towards the Malayan *A. baezi* Gater. This is well shown in the wing spotting, the subcostal spot being indicated in only 10% of specimens of the Malayan species (Gater, 1933), in 80% of Borneo specimens, and apparently in all specimens of *A. gateri*. In the shape of the processes of the 9th tergite of the male terminalia, the Borneo form is closest to the latter. In view of the identical morphology and bionomics of the larvae, the small degree of difference between the adults, the geographic distribution, and the intermediate condition of the Borneo form, it seems that *A. gateri* is best considered a geographic subspecies of *A. baezi*. The Borneo form appears to represent yet another such subspecies, but the differences involved are so slight that it is here identified with the Philippine form, pending more detailed examination of all three.

It is of interest to note that a similar trend of subspeciation, with more pale-winged forms distributed along a Malaya-Philippines cline, is shown by at least two other species described below. (See pp. 103 and 110.)

On present information, the distinctive characters of the two subspecies are as given in Table 1.

TABLE 1.

Character	<i>A. baezi baezi</i> Gater.	<i>A. baezi gateri</i> Baisas.
Subcostal spot	Present in about 10%.	Present in 80% or more.
Apical costal spot	Extends along fringe half-way to, or as far as, vein 2.1.	Does not extend past vein 1.
Processes of 9th tergite . .	Rather long and thin; more than half as long as distance between them.	Rather short and stout; about half as long as the distance between them.

Distribution.—Brunei: Kuala Belait, Brunei (local report); Sarawak: Lutong; Labuan Is.; Br. Nth. Borneo: Kimanis.

A. (A.) UMBROSUS Theobald.

THEOBALD, F. V., 1903.—*Mono. Culic.*, 3, p. 87.

Nec. STANTON, A. T., 1912: *J. Lond. School Trop. Med.*, 2, pt. 1, p. 3.

GATER, B. A. R., 1935.—*Aids to the Identification of Anopheline Imagines in Malaya*.—, 1934.—*Ibid.*

CHRISTOPHERS, S. R., 1933.—*Fauna of British India. Diptera* 4, p. 163 (in part).

SWELLENGREBEL, N. H., and RODENWALDT, E., 1932.—*Die Anoph. von Ned. Ostind.*

Type locality.—Penang, Federated Malay States.

Synonym. *A. novumbrosus*. STRICKLAND, C., 1916.—*Ind. J. Med Res.*, 4, p. 271.

Specimens examined.—Thirteen females, three males, ten larvae.

Female.

Labium (Fig. 9*b*) dark, rather shaggy near base. Palps (Fig. 9*b*) dark, shaggy, but thinner than in *A. barbirostris*. Clypeus bare. Antenna with a few scales on seg. 2, a dark tuft on seg. 3. Vertex narrow; vertical pale spot with long, narrow, upright scales at the anterior margin and successively shorter forked scales posteriorly.

Mesonotum very dark, with a blue-grey bloom when viewed from above; anterior margin with a central tuft of narrow pale scales, and lateral tufts of broad dark scales; there may be a few pale scales on the inner side of the lateral tufts. Pleura dark with some grey areas; pr. s. 3-4; ust. s. 1-3; l. st. s. 2-3; sp. s. 2-5.

Wing (Fig. 9*a*): Costa dark with small to minute subcostal spot (rarely absent), and small apical pale spot, the latter involving vein 1 and, to a varying degree, 2.1. Vein 1 dark with small to minute sector pale spot (rarely absent) and an apical pale spot. Vein 2 dark or mixed pale and dark with two dark spots; 2.1 usually with small subapical pale spot; 2.2 with a pale sub-basal spot. Vein 3 pale or mixed, with a large dark basal spot. Vein 4 dark on basal half, remainder pale or mixed, a dark spot at r-m and sometimes another apically; 4.1 and 4.2 dark at the fork, 4.2 dark apically. Vein 5 dark on the basal half, remainder pale; 5.1 with dark spots at m-cu and apex, usually a few dark scales basally; 5.2 with a large dark spot at apex. Vein 6 with prominent central dark spot, and a smaller one at apex. Remigium dark. Fork cell index approx. 1.5. Fringe with only one pale area, between veins 2.2 and 3.

Legs: Femora and tibiae pale beneath; mid and hind tibiae pale at apices, most prominent on latter. Fore tarsi (Fig. 9*c*) with small apical pale bands of decreasing size on segs. 1-3, and sometimes seg. 4. Mid and hind tarsi similar to fore, but with smaller bands; hind tarsi (Fig. 9*d*) usually with very small basal bands on segs. 4 and 5.

Abdomen entirely without scales.

Male.

Generally similar to female. Antenna without scales. Propleural hairs 4-6. Fore tarsi with small basal bands on segs. 2-4. No apical dark spot on wing veins 3, 4.2, and 6.

Terminalia: Phallosome (Fig. 9*f*) long, with very long, narrow, curved leaflets, the longest approximately equal to the phallosome. Dorsal lobe of harpago with a club, ventral lobe with a strong apical spine and a shorter external spine, the latter slightly longer than the club (Fig. 9*e*). Processes of the 9th tergite rather thin, about half as long as the distance between them.

Larva.

Head (Fig. 9g): ic. occasionally simple, but usually bifid or trifid at the tip; oc. with 12-20 branches; pc. short, simple or with up to four branches; sut. 2-5 branched; t.sut. 4-8 branched. Antennal hair with 15-25 branches. Shoulder hairs (Fig. 9i): is. short, simple or bifid towards the tip; cs. long, 6-10 branched; os. simple, longer than is. Pleural hairs: ppl. with 3 long simple, 1 very short, many branched; mpl. with 2 long simple, 1 short 2-3 branched, 1 very short simple or bifid; mtl. similar to mpl. Mt. palm. not developed, branches filamentous.

Abdominal palmate hairs not developed on segs. I and II, rudimentary on segs. III, VI and VII, and fully developed with weakly differentiated filaments, on segs. IV and V (Fig. 9h). Fan-shaped plate of the spiracular apparatus drawn out into a long "stigmatal club".

Biology.

Larvae were found only in the jungle, usually in deep shade, but occasionally extending to the more open conditions along the jungle fringe and always in peaty water with much leaf mould. Adults could be taken biting during the day in deep jungle shade, and in the open and in native houses during early evening. Five specimens dissected showed no parasites present in guts or salivary glands.

This species has been incriminated as a vector in Malaya (Hodgkin, 1936), and, from Borneo, Roper (1914) and local hygiene reports record natural infections in "*umbrosus*"; it must therefore be considered as a vector of some importance.

Notes.

It has long been recognized that the name *A. umbrosus* covers a group of at least two, and probably more, closely related species. This was noted by Gater (1935), who described under this name "what is taken to be this species in Malaya". A later reference (Gater, 1936) states that this common *umbrosus*-like species is a new and unnamed form and differs from the true *A. umbrosus* Theo.; also that *A. novumbrosus* Strick. is apparently indistinguishable from the latter. This situation is readily explained on the basis of the synonymy of *novumbrosus* and *umbrosus*, further evidence for which has been obtained by examination of the *umbrosus*-like forms of N.W. Borneo, which appear to correspond with those of Malaya.

The Borneo forms fall in three distinct species, here referred to as *A. umbrosus* and *species A* and *species B* near *umbrosus*. The first is readily identified with "*A. novumbrosus* Strick.", by its very distinct larval characters, the second is apparently identical or very similar to, the unnamed species of Gater (1936), and the third appears to be as yet undescribed. However, comparison of "*A. novumbrosus*" specimens with the original description of *A. umbrosus* (Theobald, 1903) shows no important differences, and further information about the type specimen of the latter, supplied by Mr. Oldroyd of the British Museum, convinces me that the two species are not separable. The only clear-cut distinction mentioned in the literature is in the larval characters, and, in fact, the specific status of *A. novumbrosus* was established on this basis (Strickland, 1916). It seems highly probable that the original description of the larva of *A. umbrosus* (Stanton, 1912) referred in fact to Gater's unnamed species* and failure to realize the separate identity of this species led to the subsequent establishment of *A. novumbrosus*.

Adults of *umbrosus* (as here defined) are readily distinguished from related forms by the presence of propleural hairs and the small tarsal bands on all legs. These characters also appear in Theobald's type specimen of *umbrosus*; the reduced wing spots of the latter fall within the range of variation found by me in Borneo specimens. If *novumbrosus* is to stand as a valid species, it would be necessary to prove the existence of another species with identical adult characters, and a larva which has no palmate hairs. Such a correlation, however, has never been definitely recorded.

It should be noted that such a combination of characters is described by Christophers (1933) and Swellengrebel and Rodenwaldt (1932) from India and N.E.I. respectively,

* Now known as *A. letifer* Gater; see footnote p. 95.

but it seems doubtful if their descriptions were based on homogeneous material. In any case, the "*umbrosus*" of the latter authors possesses certain features, principally the scaling on the coxae and the fringe spot opposite vein 2-1, which would indicate a new, unnamed form. However, the only specimens of N.E.I. "*umbrosus*" examined by me were *species A* and *species B* near *umbrosus*.

From the account given by Roper (1914) of variation in "*A. umbrosus*" it seems probable that at least the 30% of his specimens which lacked the subcostal spot were true *umbrosus*, and, considering the comparative rarity of this feature in my specimens, many of the remaining 70% must also have been of this species.

It is obvious that the group of *umbrosus*-like forms is badly in need of revision by someone with facilities for examining a large series of specimens from a wide variety of sources within the Oriental region. On present information, however, their principal distinctive characters are as given in the list below. (The larva of *A. brevipalpis* has been included because of its close resemblance to some members of this group.)

Adult.

Wing spotted, but without scattered pale scales on basal half of costa; abdomen without dark ventral scale tuft on seg. VII.

A. Palps without pale bands.

1. *A. umbrosus* Theo.: Propleural hairs present; tarsi with small pale bands on all legs; coxae without scales; male phallosome with very long, narrow leaflets.
2. *Sp. A* near *umbrosus*: Propleural hairs absent; pale bands on hind tarsi only; coxae without scales; ust. s. 4-6.
3. *Sp. B* near *umbrosus*: similar to preceding but larger; coxae with scales; ust. s. about 15.
4. *A. baezi* Gater: Propleural hairs present; tarsi unbanded.

B. Palps with pale bands.

5. *A. separatus* Leicester: Phallosome with leaflets.
6. *A. hunteri* Strick.: Phallosome without leaflets.

Larva.

Abdominal segments I-III and VI-VII without palmate hairs.

A. Palmate hairs present on segs. IV and V.

1. *A. umbrosus* Theo.: Stigmal club present.

B. Palmate hairs entirely absent.

2. *Sp. A* near *umbrosus*: pc. 2-3 branched near base; oc. 4-10 branched; cs. 4-8 branched.
3. *Sp. B* near *umbrosus*: not known.
4. *A. similissimus* Strick.: oc. 50-60 branched.
5. *A. baezi* Gater: pc. simple; lateral hair of abd. IV 6-12 branched; one antennal sabre notched at tip.
6. *A. brevipalpis* Roper: pc. rather long, 1-7 branched distally; oc. 7-12; cs. 3-7 branched.
7. *A. separatus* Leicester: pc. short, simple; oc. 7-16 branched; cs. 10-14 branched; lateral hair of abd. IV 2-5 branched; t. sut. 4-8 branched.
8. *A. hunteri* Strick.: similar to preceding but t. sut. 2-3 branched.

Distribution.—Brunei: Kuala Belait; Br. Nth. Borneo: Membakut (Roper).

A. SP. A. near UMBROSUS.

Specimens examined: Seven females, eight larvae.

This species closely resembles *A. umbrosus* Theo. but differs from it in the characters given below.

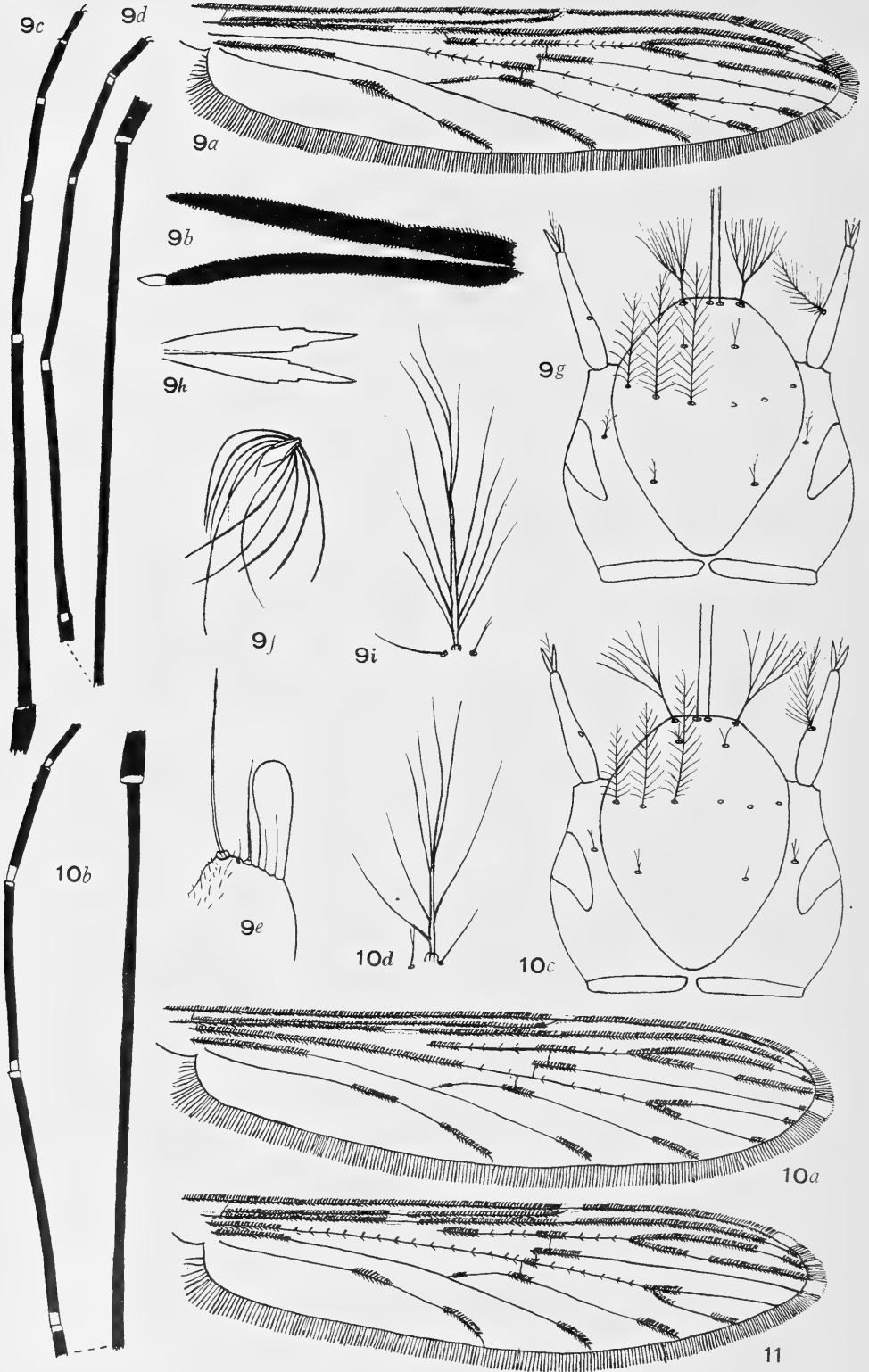
Female.

1. Scales of the vertical pale spot rather uniform in length and shape; narrow scales at anterior margin few in number or absent.

2. Anterior margin of mesonotum with central tuft of rather shorter scales. Pr. s. absent; ust. s. 3-6; 1st s. 2-5.

3. Wing (Fig. 10a) generally paler; subcostal spot and sector pale spot of vein 1 both present in all specimens examined, the former sometimes slightly involving vein 1. Vein 4 usually without dark spot at r-m.

4. Fore and mid tarsi dark, or with faint indications of minute pale bands; hind tarsi (Fig. 10b) with narrow pale bands at apices of segs. 1-4, very small on the latter, and narrow basal bands on segs. 2-5, very small on the latter.



Larva.

Head (Fig. 10*c*): ic. simple or divided into 2-3 branches at about three-fourths the distance from base; oc. 4-8 branched; pc. divided at base into 2-3 branches; sut. 2-5 branched; t. sut. 2-3 branched. Antennal hair 8-15 branched, two-thirds the length of the antenna.

Shoulder hairs (Fig. 10*d*): is. short, simple or divided at about half-way into 2 or 3 branches; cs. long, 5-8 branched; both with weak root. Mt. palm. not developed, with 3-5 filamentous branches. Hair no. 1 of mesothorax weakly developed, with 10-14 branches. Pleural hairs: ppl. with 3 long simple, 1 very short with 4-8 spiny branches; mpl. with 2 long simple, 1 short simple or bifid, 1 very short simple or rarely bifid; mtpl. with 2 long simple, 1 short, 2-4 branched, 1 minute simple.

Abdominal palmate hairs not developed on any segment. Hair no. 0 developed, but very small, on abd. II-VII. Lateral hair of abd. IV and V 2-3 branched. A small chitinous plate present on the ventral surface of abd. VII. Psp. 2-3 branched.

The male was not seen.

Biology.

Larval and adult habits closely resemble those of the preceding species, and the two were often found together. The larvae did, however, appear to favour more open conditions and were occasionally found in open grassy swamp away from the jungle. Only one adult was dissected; both gut and glands were negative.

Remarks concerning the vector potentialities of the preceding species apply equally well here.

Notes.

The distinctive characters of this species are given in Table 1; the adult characters are quite clear-cut, but in the larval stage it is sometimes difficult to separate this species from *A. brevivalpis* (see p. 77).

This appears to be the species described as "*A. umbrosus*" by Gater (1934 and 1935), agreeing well in all points, except the wing fringe. None of the Borneo specimens showed a pale area at the termination of vein 2.1, and if such a spot occurs, it must be very uncommon. Possibly a subspecific difference is involved.

The Malayan form has recently been described and named by Gater* (Hodgkin, personal communication), but I can find no reference to it in the literature and the provisional name above has therefore been used.

Distribution.—Brunei: Kuala Belait.

A. SP. B NEAR UMBROSUS.

Specimens examined: Three females.

Very similar to the preceding species, differing in the following characters:

Female.

1. Noticeably larger; wing length 4.5-4.7 mm., as compared to 3.8-4.2 mm. in *sp. A* near *umbrosus*.

2. Vertical pale spot small, bordering a distinct bare area.

3. Upper sternopleural hairs weak, about 15 in number.

4. Wing (Fig. 11) with pale fringe spot at vein 2.1, separated from the apical spot by a few dark scales. Sector pale spot on vein 1 and subcosta and subcostal spot all prominent, the latter partially involving vein 1.

* Later information (Reid, personal comm.) shows that the Malayan species was named *A. letifer* by Gater in a manuscript description, subsequently lost by enemy action.

Text-figures 9-11.

Fig. 9.—*A. umbrosus* Theobald. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Fore tarsus $\times 55$. (d) Hind tarsus $\times 55$. (e) Harpago $\times 570$. (f) Phallosome $\times 420$. (g) Larval head $\times 120$. (h) Leaflets from abdominal palmate iv $\times 910$. (i) Shoulder hairs $\times 205$.

Fig. 10.—*A. sp. A. near umbrosus*. (a) Wing $\times 55$. (b) Hind tarsus $\times 55$. (c) Larval head $\times 120$. (d) Shoulder hairs $\times 205$.

Fig. 11.—*A. sp. B. near umbrosus*. Wing $\times 42$.

5. Mid coxae with patch of narrow pale scales, fore and hind coxae with a few scattered scales. Hind tarsi with small apical pale bands on segs. 1-4, small basal bands on segs. 4 and 5.

The male and larva were not seen.

Notes.

Two of the specimens described above were taken biting during the day in jungle shade; the other was found in a collection of Oriental Anophelines in the School of Tropical Medicine, Sydney University, and came originally from Poeroek Tjauh, Dutch Borneo. Despite the small numbers examined, their characters are quite distinct and appear worthy of specific status; no attempt is here made, however, to describe fully and name this species as material to hand consists of several females only.

An apparent earlier reference to this form is the mention by Roper (1914) of a large variety of *A. umbrosus* from Nth. Borneo. This "variety" was also distinguished by the presence of a fringe spot at vein 2·1, and seems most likely to have been the above species. No other reference to such a form can be found in the literature and the species may be confined to Borneo; however, undescribed *umbrosus*-like forms are known to occur in Malaya, and possibly it will be found there.

Distribution.—Brunei: Kuala Belait; Br. Nth. Borneo: Membakut (Roper).

A. (M.) KOCHI Dönitz.

DÖNITZ, W., 1901.—*Insectenborse*, 18, p. 36.

Type locality: Padang, Sumatra.

Specimens examined: Thirty-three females, seven males, numerous larvae.

Female.

Labium (Fig. 12*b*) dark on basal half, pale golden on apical half, with variable interruptions of dark or golden scales, and usually a small dark ring distally behind the labella; a ventral tuft of dark scales at base. Palps (Fig. 12*b*): seg. 5 with narrow dark basal band, remainder golden; seg. 4 with narrow dark basal band, followed by slightly broader golden band, apical two-thirds white; seg. 3 narrowly dark at base, then golden or mixed golden and black; apical half white; the golden area often with narrow dark band distally; seg. 2 white at apex, remainder dark with variable admixture of golden scaling. Antenna with small pale scales on seg. 2; seg. 3 with a white tuft and a few dark scales.

Mesonotum pale with prominent dark spots in posterior angle of the fossae and in front of, and extending on to, the scutellum; also smaller spots in front of, and above, the wing roots and in anterior angles of the fossae; anterior margin with central tuft of mixed broad and narrow pale scales, and lateral tufts of broad pale scales with some dark scales low down on anterior face; remainder of mesonotum clothed in pale scales, broadest and most numerous anteriorly, in the fossae, and along the lateral margins. Pn. 1 with tufts of dark and golden scales. Pleura dark with grey areas; pr. s. 2-4; ust. s. and l. st. s. 2-5; sp. s. replaced by several small pale scales. Small patches of pale scales associated with ust. s., um. s., and pa. s.

Wing (Fig. 12*a*): Extensively pale; dark spots very small. Costa with prominent prehumeral pale area, often extending to wing base, followed by four small pale spots and long subcostal, preapical, and apical pale spots; humeral and presector or sector and accessory sector pale areas may be confluent. Sc. with presector and middle dark spots. Vein 1 with 1 or 2 dark spots in the sector region, two small spots at the centre, two more at subapical region, apical dark spot undivided. Vein 2 pale or with 1 or 2 small dark spots; 2·1 with sub-basal dark spots and 1 near centre; 2·2 with sub-basal, central, and subapical dark spots. Vein 3 with sub-basal and subapical dark spots. Vein 4 pale with dark spots at centre and distally and sometimes another between these; 4·1 and 4·2 with large dark sub-basal spot and small dark subapical. Vein 5 pale with a dark spot near base; 5·1 with a dark spot on each side of m-cu, and one subapically; 5·2 dark near apex. Vein 6 dark at apex, centre, and near base. Remigium pale. Fringe mostly pale with dark spots between the apices of all veins from 2·1 to 5·1, 1 or 2 dark spots between 5·1 and 5·2, 2 between 5·2 and 6, and another beyond 6.

Legs: Coxae with pale scales. Femora and tibiae pale at apices, the latter basally also; bands minute on fore and mid legs, most prominent on hind legs. Femora, tibiae, tarsi 1 and occasionally tarsi 2, liberally speckled with white. Fore tarsi with incomplete pale apical bands on segs. 1-3 and sometimes 5, pale basally on segs. 2-4; mid tarsi pale apically on all segs., bands on segs. 1-4 minute; hind tarsi with narrow pale apical bands on seg. 1, broad apical bands on other segs.; also broad basal bands on segs. 3 and 4, and a narrow basal band on seg. 5.

Abdomen: abd. II-VIII with flat golden scales dorsally towards the posterior margin, most profuse on seg. VIII and cerci. Ventrally, abd. II-VII with dark outstanding tufts on either side of centre line towards the posterior margin, seg. VIII with a few golden scales laterally.

Male.

Generally similar to female. Proboscis more extensively pale scaled, dark interruptions very variable. Antenna with some scales on seg. 3.

Terminalia: Coxites heavily scaled. Phallosome short with 3-5 leaflets on each side, some of the larger ones with 1 or 2 small serrations. Harpago (Fig. 12c) with apical spine a little longer than club and 1-3 shorter setae internally or externally about its base.

Larva.

Head (Fig. 12d): ic. with short, fine side hairs, simple or rarely bifid on one side; oc. fine, usually simple but sometimes with 1, 2 or rarely 3 branches; pc. placed wide apart, simple or occasionally bifid on one side; sut. and t. sut. 1-3 branched. Antennae usually lightly pigmented.

Shoulder hairs (Fig. 12e): is. weak with 2-10 branches; cs. with 8-18 branches and fairly prominent root. Pleural hairs: ppl. with 3 long simple, 1 short simple, or bifid; mpl. with 2 long simple, 1 short simple, or rarely bifid, 1 minute simple; mtpl. with 2 long simple, 1 short 2-3 branched, 1 minute simple. Mt. palm. developed with unpigmented lanceolate leaflets.

Abdominal palmate hairs: abd. 1 small, weak, with filamentous or flattened branches, rarely with lanceolate leaflets; abd. 11 weakly developed, with clear lanceolate leaflets; abd. III-VI developed with short, pointed filaments, broad basally; rarely with lanceolate leaflets; pigment light, filaments clear; abd. VII smaller and less well differentiated. Lateral hairs on abd. IV and V 1-3 branched. Psp. 2-4 branched.

Biology.

This was one of the commonest and most widespread species found in the area, the larvae being found to breed in almost any collection of water not subject to heavy shade. Typical situations were drains, buffalo wallows, padi fields, seepages, etc., and even in empty tins. Vegetation was apparently not essential, and extremely muddy water was tolerated.

The adult was never observed to bite man, but during the first few hours of darkness many could be caught in the vicinity of tethered animals. The species appears to be almost entirely zoophilic in its blood preferences, though it may take human blood in areas where animals are scarce. Two specimens dissected showed no parasites in guts or glands.

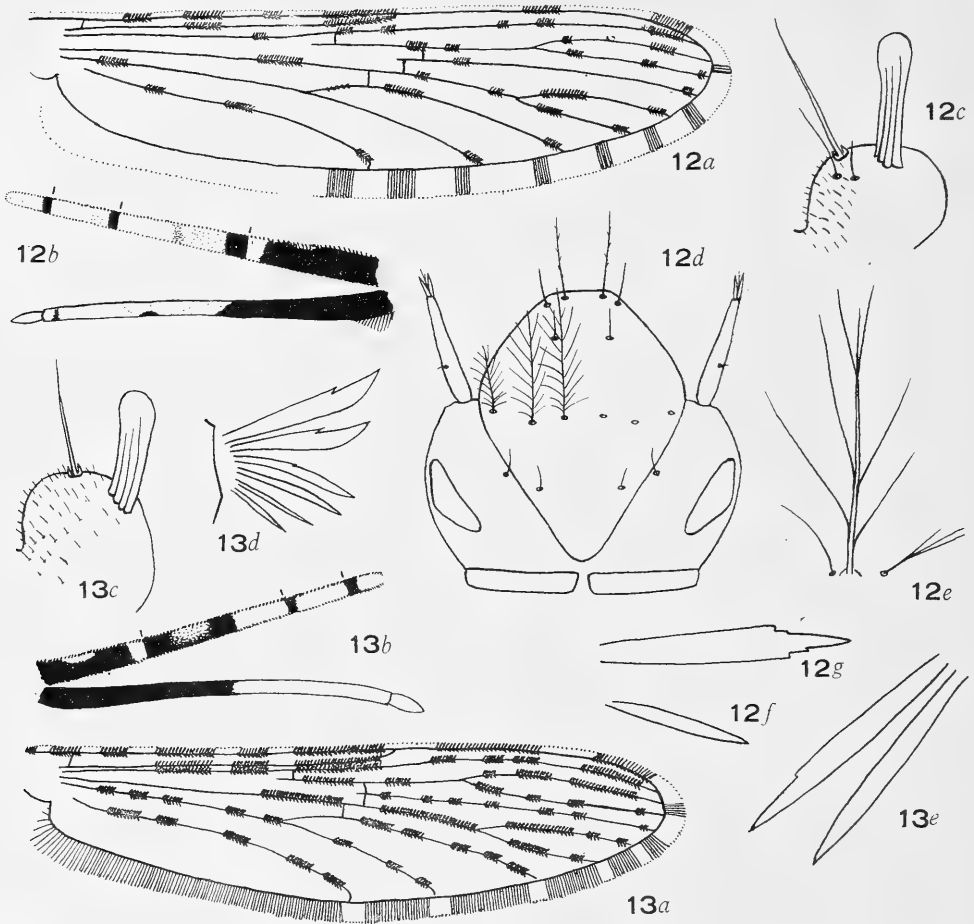
Its zoophilic habits would appear to eliminate this species as a possible vector of malaria in this area.

Notes.

The adult is readily identified by the prominent ventral tufts on the abdomen and conspicuous ornamentation of the appendages. The larva is distinguished by the form of the inner shoulder hair and the weakly differentiated abdominal palmate hairs; from the rather similar *A. tessellatus*, it is differentiated by the presence of palmate hairs on abdominal segments I and II. The lightly pigmented antennae and clypeal hairs also offer a more easily seen and generally trustworthy criterion for separating these two species.

All specimens examined agreed well with descriptions from other areas.

Distribution.—Brunei: Brooketon; Brunei; Limbang; Lompaku Is.; Kilanis; Kuala Belait; Sarawak: Miri (Stokes); Labuan Is.; Br. Nth. Borneo: Beaufort, Kimanis, Membakut, Papar, Jesselton.



Text-figures 12 and 13.

Fig. 12.—*A. kochi* Dönitz. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Larval head $\times 120$. (e) Shoulder hairs $\times 290$. (f) Leaflets from abdominal palmate ii $\times 970$. (g) Leaflets from abdominal palmate iv $\times 970$.

Fig. 13.—*A. tessellatus* Theobald. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 590$. (d) Leaflets of phallosome $\times 970$. (e) Leaflets from abdominal palmate iv $\times 970$.

A. (M.) TESSELLATUS Theobald.

THEOBALD, F. V., 1901.—Mono. Culic., 1, p. 175.

Type locality: Taiping, Perak, Federated Malay States.

Specimens examined: Twelve females, five males, eighteen larvae.

Female.

Labium (Fig. 13b) dark basally, apical half pale golden with a small, dark ring distally behind the labella. Palpi (Fig. 13b): seg. 5 dark on basal half, golden apically; seg. 4 with narrow dark basal band, remainder white; seg. 3 with basal half dark, broken by dorsal patch of white scales, apical half white; seg. 2 dark with narrow apical pale band and central patch of pale scales dorsally. Antennae with a few scales on seg. 2 and a white tuft on seg. 3.

Mesonotum with ornamentation similar to *A. kochi*; anterior margin with pale central tuft and lateral tufts of pale and dark scales; remainder with a few narrow hair-like scales. Pn. 1. with very small dark tufts. Pleurae dark with grey areas; pr. s. 1-2; ust. s. 2-4; l. st. s. 3-7 in a compact tuft; sp. s. absent.

Wing (Fig. 13a): Costa with usual 8 pale spots, including one in accessory sector region; prehumeral pale spot sometimes absent; apical pale spot extending to apex of vein 2-1. Vein 1 with dark spots in presector and sector regions; 1-2 under middle dark spot, sometimes 1 or 2 under subcostal spot, 1-3 in preapical region, and 1 near the apex. Vein 2 with a dark spot each side of the base of vein 3; 2-1 largely dark, with 1 or 2 pale spots; 2-2 with basal and apical dark spots and 1-2 others between them. Vein 3 with 5-7 dark spots. Vein 4 pale basally with 1 or 2 dark spots on the central one-third and a very long dark spot before the fork; 4-1 and 4-2 with basal and subapical dark spots. Vein 5 with 4-5 small dark spots; 5-1 with 3-4 spots distal to m-cu; 5-2 with 3-4 dark spots. Vein 6 with 3-5 small dark spots. Remigium pale. Fringe pale between 2-2 and 3 and at apices of the other veins.

Legs: Coxae without scales. Femora, tibiae, tarsi I and II with conspicuous white spots; femora pale basally and minutely pale apically; tibiae minutely pale at base and apex, the latter wider on the hind leg. Tarsi: fore leg with pale apical bands on all segments, small basal bands on segs. 2-4; mid-leg similar but the bands minute and the basal bands sometimes absent; hind leg with pale apical bands on segs. 1-4 and sometimes 5.

Abdomen: Cerci with pale scales, otherwise unscaled.

Male.

Generally similar to female. Labium dark. Abdomen with narrow pale scales dorsally on seg. VII.

Terminalia: Phallosome with 5-7 leaflets on each side, the largest of a characteristic broad, blade-like shape with 1 or 2 teeth on the inner margin (Fig. 13d). Harpago (Fig. 13c) with apical spine slightly longer than the club, and no distinct internal or external spines; the latter apparently replaced by several small hairs, set in large sockets but otherwise indistinguishable from the numerous accessory hairs.

Larva.

Head: ic. simple, rather short and stout with short side hairs; the latter, though never very long, vary from fine and inconspicuous to prominent and bushy; oc. simple, fine, and very short; pc. short and fine, simple or rarely bifid on one side; sut. 1-3 branched; t. sut. 2-5 branched.

Shoulder hairs: is. with 3-6 branches and weak root; cs. usually rather stout with 7-14 branches and a prominent root. Pleural hairs: ppl. with 3 long simple, 1 short simple; mpl. 2 long, 1 short, and 1 minute, all simple; mtpl. with 2 long simple, 1 short 2-3 branched, and 1 minute simple or rarely bifid. Mt. palm. developed with long, narrow, unpigmented, lanceolate leaflets or sometimes with flattened branches only.

Abdominal palmate hairs (Fig. 13e): abd. I undeveloped with filamentous branches; abd. II similar but sometimes with flattened branches; abd. III-VI developed with lanceolate or slightly differentiated leaflets, with long fine tips and light, even pigment; abd. VII smaller, usually with lanceolate leaflets. Psp. 2-5 branched. Lateral hair on abd. IV bifid, on abd. V 2-3 branched.

Biology.

Larvae of this species were less common than those of the preceding, but frequented similar breeding sites, generally small pools, drains, etc., usually open to the sun, and with either clean or muddy water. The adults were readily attracted by human bait in areas where animals were scarce, but in the presence of water-buffaloes, these seemed to be preferred. Dissections showed no parasites in eight guts and ten salivary glands.

Notes.

The adult is readily identified by the conspicuous ornamentation of palps and proboscis and the spotted wings, being rather similar to *A. kochi* but lacking the ventral

scale tufts. The larvae of these two species are also rather similar; for their distinguishing features see under *A. Kochi* (p. 96).

The Borneo specimens appeared to show no variation from the usual description of this species from other countries.

Distribution.—Brunei: Kuala Belait; Sarawak: Miri (Stokes); Labuan Is.; Br. Nth. Borneo: Jesselton, Membakut (Roper).

A. (M.) LEUCOSPHYRUS BALABACENSIS Baisas.

BAISAS, F. E., 1936.—*Philipp. J. Sci.*, 59, 65.

Type locality: Balabac Is., Philippine Is.

Specimens examined: Fifteen females, twelve males, numerous larvae.

Female.

Labium (Fig. 15*b*) dark, rather shaggy towards the base ventrally. Palps (Fig. 15*b*) with narrow pale apical bands on segs. 2-4 and a broader apical band on seg. 5, the latter equal to or somewhat wider than the subapical dark band. Antennae with pale scales on seg. 3. Vertical chaetae arranged in a more or less regular single row (Fig. 15*d*). Palp/proboscis ratio 0.98-1.03, mean 1.01.

Mesonotum dark with a greyish bloom, and a conspicuous pattern of paired dark spots, one in the posterior angle of the fossa, one behind this and slightly lateral to it, and one above the wing root, together with a central dark area in front of the scutellum; anterior margin with central tuft of pale narrow scales, and lateral tufts of broader scales, mostly dark; a few broad flat scales usually present in the fossae and some pale erect scales laterally in front of the wing roots. Halteres conspicuously white above, black below. Pleura dark with some lighter areas; pr. s. 1 or 2, rarely 3; spirac. s. 1 or 2, one sometimes replaced by a flat scale.

Wing (Fig. 15*a*): Costa with usual pale areas; prehumeral pale spot sometimes absent; a partial or complete accessory sector pale spot usually present; apical pale spot extends along fringe only to apex of vein 2.1. Vein 1 with the presector dark spot on at least one wing, divided by 1 or 2 pale areas, the middle and subapical dark spots variably subdivided. Vein 2 dark basally; 2.1 and 2.2 dark at base with 2-3 other dark spots. Vein 3 with 6-7 dark spots. Vein 4 with dark or mixed scaling, and definite dark spots at the crossveins and before the fork; 4.1 and 4.2 with central and apical dark spots. Vein 5 pale basally with 3-5 dark spots; 5.1 with 5-6 dark spots, 5.2 with 3-4. Vein 6 with 3-7 dark spots. Fringe pale between 2.2 and 3 and at apices of 4.1-5.1, usually at 5.2, and often between 5.2 and 6. The long spot between 2.2 and 3 may be broken into a small spot at the apex of each vein or at the latter only. Bases of the fork cells approximately level or pf. slightly further from the wing base; fork cell index 1.76 (1.7-1.8); af. petiole index 0.61 (0.5-0.7); pf. petiole index 1.1 (0.9-1.2).

Legs: Coxae without scales. Femora, tibiae, tarsi I and sometimes tarsi II, with conspicuous white spots. Hind femur with narrow pale apical band, hind tibia with narrow basal band and broad white apical band; the latter, in conjunction with a broad basal band on tarsus 1, forms the conspicuous knee spot which characterizes this species and its near relatives. Fore tarsi (see Fig. 14*d*) with seg. 2 usually spotted, segs. 1-5 with pale apical bands, segs. 2-4 with pale basal bands; mid tarsi (see Fig. 14*e*) with narrow apical bands on segs. 1-4, often on seg. 5 also; hind tarsi (Fig. 15*c*) with very broad basal pale band on seg. 1, narrow apical bands on segs. 1-5, and a small basal pale patch or band on seg. 4 and sometimes 5; seg. 2 sometimes spotted.

Abdomen: Dorsal surface with numerous golden scales on seg. VIII; ventral surface with a dark tuft on seg. VII, and some flat golden scales on seg. VIII. Cerci with golden scales.

Male.

Generally similar to female. Fore legs without basal banding on segs. 1-3, seg. 4 basally banded or entirely pale, seg. 5 pale. Wing with prominent accessory sector pale spot on costa; presector dark spot on vein 1 simple or divided. Abdomen with profuse golden scaling on dorsal surface of seg. VIII and a few dark scales ventrally on segs. VII and VIII.

Terminalia: Phallosome with 8 or 9 blade-like leaflets on each side, several of the larger ones with serrations (see Fig. 14j). Harpago (see Fig. 14i) with club and apical spine slightly shorter than club; other spines variable; usually 1 internal spine about half the length of the apical spine, and a short seta below it on the face of the lobe; however, either of these may be duplicated or the short seta may be absent, on one or both harpagones.

Larva.

Head (see Fig. 14k): ic. simple or with fine side hairs; oc. simple, about one-third length of ic.; pc. simple; sut. 1-3 branched; t. sut. 2-3 branched. Shoulder hairs (see Fig. 14l); is. 10-24 branched and prominent pigmented root; cs. 8-14 branched with prominent root, often joined to that of is.; os. short, simple. Mt. palm. weakly developed with long stem and lanceolate leaflets. Pleural hairs all simple, except for a short 2-3 branched hair in the metapleural group.

Abdominal palmate hairs (see Fig. 14m) rather variable; abd. I small and undeveloped; abd. II developed with lanceolate leaflets, sometimes with poorly differentiated filaments; abd. III-VI developed with variable degree of differentiation, from a short, pointed filament with broad base to a practically undifferentiated condition; abd. VII smaller, usually lanceolate.

Biology.

The typical breeding place of this species as recorded from other countries is in deeply shaded pools, under jungle cover. Although the above subspecies was recorded on several occasions from such places, heavy larval concentrations were frequently found in open, lightly shaded or sunny, situations, in bomb craters, wheel ruts, and miscellaneous pools; these usually had a fine silt bottom and clear water. However, McArthur (1946) records *A. leucosphyrus* as an almost exclusive jungle breeder in Nth. Borneo, and it seems likely that the atypical breeding sites recorded above were due to abnormal seasonal conditions, possibly the drying-up of jungle seepages.

The adult was rarely taken in the field, due probably to its shy habits and late flight period. Dissections of seven females, taken with human bait, were all negative. McArthur (op. cit.) has proved *A. leucosphyrus* to be a dangerous vector in the interior of Nth. Borneo, but there is no certainty that this was the subspecies involved, and subspecific differences in vector ability may occur.

Notes.

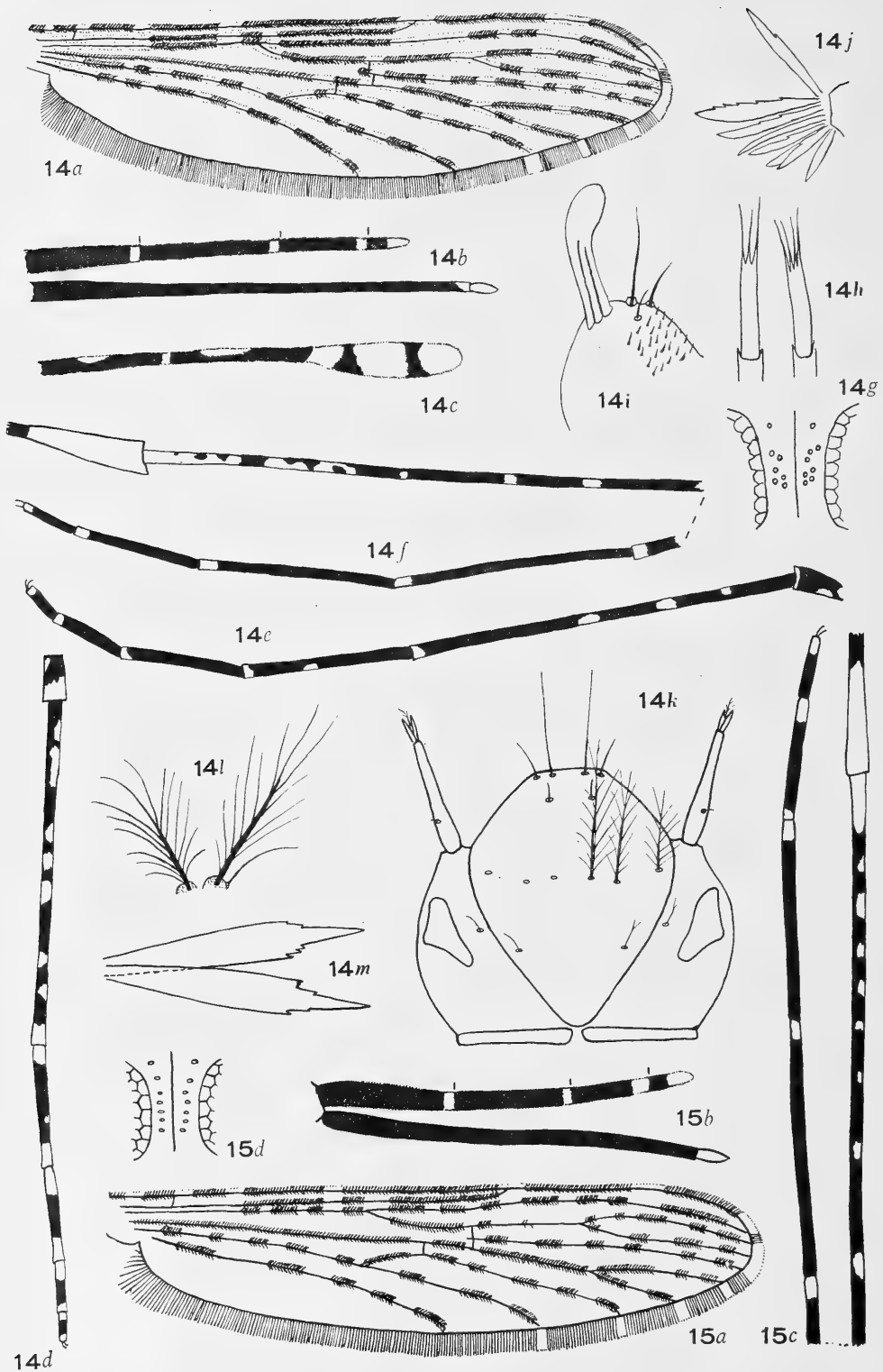
The adult is readily identified by the conspicuous pale band at the hind tibio-tarsal joint and the relatively broad pale bands on the palps; the rather similar *A. hackeri* is distinguished by its very narrow palpal bands, and the Philippine *A. cristatus* by a dark interruption to the pale tibio-tarsal band. The larva is characterized by the prominent shoulder hairs with their large pigmented roots, the simple clypeal hairs, and the developed, but weak, palmate hair on abd. II. The subspecific status was based by Baisas (1936) principally on the presence of a small basal pale band on hind tarsal seg. 4 of the adult.

This is almost certainly identical with the subspecies described by Baisas (op. cit.), from Balabac and Palawan Islands, which lie close to the north coast of Borneo. However, the characters differentiating this form from the type-form require further investigation as specimens from Malaya and N.E.I. sometimes show the basal band on hind tarsal seg. 4 and the fork cell characters appear to be rather variable. In this last character the Borneo form differs from the Philippine to a noticeable degree; possibly further subspecific differentiation has occurred, but it may also be explained by a high degree of variation between local populations. The systematic value of this character requires further investigation.

Distribution.—Brunei: Brunei; Labuan Is.; Br. Nth. Borneo: Jesselton.

A. (M.) LEUCOSPHYRUS PUJUTENSIS n. subsp.

Types: Holotype female, allotype male, six female paratypes, six male paratypes, together with cast skins of holotype and four paratypes, and one morphotype larva in Museum of



Division of Economic Entomology, Council for Scientific and Industrial Research, Canberra, A.C.T.

Type locality: Pujut, Northern Sarawak.

Specimens examined: Twenty females, twenty-two males, numerous larvae.

Female.

Closely resembles *A. l. balabacensis*, differing in the following characters:

1. Apex of labium with narrow ring of golden scales proximal to labella (Fig. 14*b*).
2. Palp/proboscis ratio 0.81-0.91, mean 0.86 (Fig. 14*b*).
3. Vertical chaetae arranged in two markedly irregular rows (Fig. 14*g*).
4. Propleural setae 3-4 (rarely 2).
5. Wing with presector dark spot of vein 1 undivided and equal in length to corresponding spot on costa (Fig. 14*a*).
6. Forked-cell index 1.5-1.7, mean 1.63.
7. Hind legs almost invariably without pale basal markings on tarsal seg. 4 (Fig. 14*f*).

Male.

Generally similar to female; differs from *A. l. balabacensis* in characters 1 and 7 above; other characters appear unreliable or were not investigated. No differences could be detected in the genitalia of the two subspecies (Figs. 14*i*, 14*j*).

Larva.

Shows no constant differences from *A. l. balabacensis*.

Biology.

The only larval breeding places recorded were pools of casual water lying in rather open situations under light to medium shade. Probably the normal habitat is similar to that of the preceding subspecies. The adult was not taken in the field.

Notes.

The characters given above separate this subspecies quite distinctly from *balabacensis*, and in the golden tip of the proboscis and the short palps, it differs from all other forms of *A. leucosphyrus* described from other countries. The arrangement of the vertical chaetae also differs quite noticeably from that described by Christophers (1933). It is difficult to make a detailed comparison with the type form, as descriptions from other countries vary considerably in some characters; it seems that there is need for further subdivision in this species if precise definition is required.

Such a subdivision has been applied to *A. leucosphyrus* in the Philippine Is., where three subspecies and one closely related species are now recognized (Russell and Baisas 1936; King and Baisas 1936). It should be noted in passing that the subspecies from Luzon Is., referred by Russell and Baisas (op. cit.) to the subspecies *A. l. leucosphyrus*, is most probably quite distinct from it. For instance, the relative positions of the bases of the forked cells do not correspond with that usually shown for the type form (figures in Theobald 1903, Gater 1935, Swellengrebel and Rodenwaldt 1932), in which the anterior fork is nearer the wing base than the posterior fork; the banding of the front tarsal segments also appears to be rather distinctive.

The actual status of the form described here is somewhat uncertain but it is morphologically quite distinct from *A. l. balabacensis*. Statistical analysis of the palp/proboscis ratio shows a high order of significance (P less than 0.01); the forked cell difference was not statistically significant but is suggestive and the other characters described, particularly those of wing, proboscis, and tarsi, give a complete separation

Text-figures 14 and 15.

Fig. 14.—*A. leucosphyrus pujutensis* n. subsp. (a) Wing × 55. (b) Palp and proboscis × 55. (c) Male palp × 55. (d) Fore tarsus × 55. (e) Mid tarsus × 55. (f) Hind tarsus × 55. (g) Vertex pattern × 205. (h) Pharyngeal teeth × 910. (i) Harpago × 570. (j) Leaflets of phallosome × 910. (k) Larval head × 120. (l) Shoulder hairs × 205. (m) Leaflets from abdominal palmate iv × 570.

Fig. 15.—*A. leucosphyrus balabacensis* Baisas. (a) Wing × 55. (b) Palp and proboscis × 55. (c) Hind tarsus × 55. (d) Vertex pattern × 205.

of all specimens examined. The question remains as to whether this is a geographic subspecies or a true species and until further distribution records are available, no decision can be made. Those which are available seem to indicate a subspecific distribution, as little or no overlapping of the two forms was observed. The boundary appears to lie in southern Brunei, with *balabacensis* to the north, and *pujutensis* to the south; one specimen from Seria, in this boundary zone, showed apparently intermediate characters. However, a male specimen from Beaufort, in Br. Nth. Borneo, appears to be *pujutensis*, and Edwards (1921) mentions a specimen, collected by Roper and presumably from Membakut, Br. Nth. Borneo, which had very short palps and may therefore have been this form. This would indicate either a wide zone of overlapping or a specific distribution. For the present it seems best to consider this form as a subspecies, until it can be shown whether the two forms exist together without interbreeding.

It is interesting to note that some records from eastern Borneo and almost all records from Celebes, relate to "*var. hackeri*" (Swellengrebel and Rodenwaldt, 1932). It seems unlikely that this is the true *hackeri*, a rather rare Malayan and Sumatran species of restricted breeding habits, but may represent a short-palped form, related to *pujutensis*, or even identical with it, as the golden tip to the proboscis is very inconspicuous, unless close examination is made. However, *hackeri*, as described from the N.E.I. by Swellengrebel and Rodenwaldt (op. cit.), has a characteristic palpal ornamentation, and if the above records conform to this description, they may indicate the existence of yet another species or subspecies.

The distribution of the known members of the *leucosphyrus* complex is:

1. *A. cristatus* King and Baisas; Mindanao, Philippine Is.
2. *A. hackeri* Edwards; Malaya; Sumatra.
3. *A. leucosphyrus leucosphyrus* Dönitz; Java to eastern India.
4. *A. l. balabacensis* Baisas; Nth. Borneo; Balabac, Palawan, Philippine Is.
5. *A. l. pujutensis* n. subsp.; Sarawak, Brunei, Borneo. Limits of distribution not known.

The following are forms which may possibly be distinct and seem worthy of further study:

6. "*A. l. leucosphyrus*" (Russell and Baisas, 1936): Luzon, Philippine Is.
7. "*A. l. leucosphyrus*" (Christophers, 1933): Western India; Ceylon. This form is included here on the basis of its geographic separation from other forms and the insistence of Theobald (1903, 1907, 1910) on the separate identity of his "*Myz. elegans*" James, from the west coast of India; this was synonymized with *leucosphyrus* by James and Stanton (1912).
8. *A. l. "var. hackeri"* (Swellengrebel and Rodenwaldt, 1932): Eastern Borneo; Celebes; Sangir and Talaud Is.

Distribution.—Brunei: Seria; Sarawak: Pujut; Br. Nth. Borneo: Beaufort.

A. (M.) KARWARI James.

JAMES, S. P., in THEOBALD, F. V., 1903.—Mono. Culic., 3, p. 102.

Type locality: Karwar, west coast of India.

Specimens examined: Six females, five males, sixteen larvae.

Female.

Labium (Fig. 17*b*) dark, shaggy on ventral surface near base. Palps (Fig. 17*b*): seg. 2 shaggy, dark with narrow apical band; seg. 3 similar but band somewhat wider; seg. 4 and seg. 5 dark on basal third, remainder pale; the pale apical band of the palp a little narrower than the subapical, both much wider than the corresponding dark bands. Antennae with a few scales on segs. 2 and 4, and a pale tuft on seg. 3.

Mesonotum dark, clothed with medium to broad pale scales, broadest in the fossae; a linear bare patch posterior to each fossa; anterior margin with central tuft of long narrow pale scales, lateral tufts of broader scales, indistinctly grouped. Pn. 1. without scales. Pleura dark, unscaled; pr. s. absent; ust. s. 2-3; 1. st. s. 1-3; sp. s. 2-4. Scutellum with pale scales on posterior margin.

Wing (Fig. 17a): Generally similar to that of the species following (*A. maculatus*). Costa without prehumeral pale spot. Vein 6 with small dark sub-basal spot, and long subapical spot, the latter covering about one-third length of vein. A fringe spot present between veins 5·2 and 6 and another long one between vein 6 and wing base.

Legs: Coxae with scales. Fore femur pale beneath on distal third, other femora and all tibiae pale beneath to a varying degree, with some pale scales at their apices, most prominent on hind tibiae. Mid and hind tibiae usually with a patch of pale scales laterally near their bases. Fore tarsi with small apical pale bands on segs. 1-3, decreasing in size distally; mid tarsi similar but bands smaller, even absent on seg. 3; hind tarsi with apical pale bands of increasing size on segs. 1-3; seg. 4 with broad apical and basal pale bands, in length about one-third and one-fourth of the segment resp.; seg. 5 entirely pale.

Abdomen: Dorsally, with a few narrow pale scales on seg. VII, more numerous and broader on seg. VIII. Ventrally, a few narrow pale scales laterally on segs. VII and VIII. Cerci with numerous broad pale scales dorsally, dark scales ventrally.

Male.

Generally similar to female. Antennae with pale tufts on segs. 3 and 4. Wing without fringe spot between veins 6 and 5·2. Legs without apical bands on seg. 3 of fore and mid tarsi. Abdomen with numerous pale scales dorsally on seg. VIII, a few on seg. VII; ventrally, seg. VIII with numerous dark scales and some pale scales laterally on segs. VIII and VII.

Terminalia: Phallosome with 5-7 leaflets on each side, these rather broad and blade-like with serrations on the lower margin (Fig. 17a). Harpago (Fig. 17c) with club and strong apical spine, about half as long again as the club; also one stout external and one to two finer internal spines, all shorter than the club; near base of internal spine is a quite large, socket-like pit, occupied by a minute seta.

Larva.

Head: ic. pigmented, long, simple with short side hairs; oc. about one-half length of ic., simple with stout side hairs; pc. equal in length to oc. but finer, simple or bifid on one side; sut. simple or bifid on one side; t. sut. with 3-6 branches, rarely simple.

Shoulder hairs: is. dark, with stout, flattened stem and rather prominent root, 19-27 branched; cs. similar but longer. Pleural hairs: ppl. with 2 long simple, 1 long and branched, 1 short with 3-5 stout branches; mpl. with 1 long branched, 1 long simple or rarely bifid, 1 short simple or with 2-4 branches, 1 minute simple; mtpl. with 2 long branched, 1 short, 3-6 branched, 1 minute simple. Mt. palm. undeveloped, with 2-7 filamentous branches.

Abdominal palmate hairs (Fig. 17e): abd. I rudimentary, with 1-5 filamentous or flattened branches; abd. II weakly developed with narrow unpigmented lanceolate leaflets; abd. III-VII fully developed, with short, blunt-tipped filaments, about one-fourth the length of the blade; pigment patchy, concentrated distally. Hair no. 5 on abd. II with 4-8 branches, usually 5 or 6. Lateral hair on abd. IV with 7-11 branches, on abd. V and VI 7-12 branches. Psp. 5-8 branched.

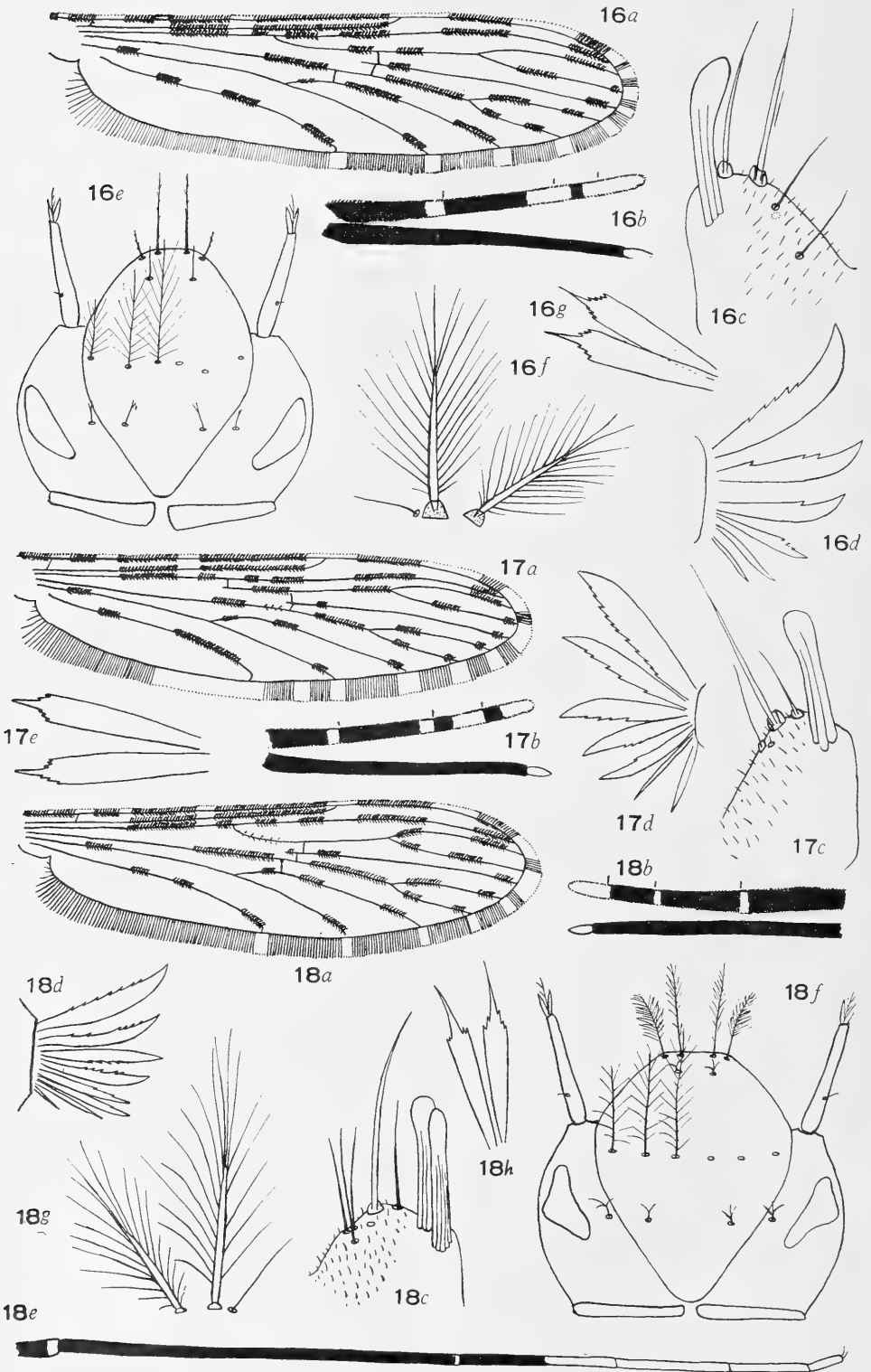
Biology.

The larvae were found usually in grassy pools or seepage water, exposed to the sun or lightly shaded. Heavy concentrations were recorded from seepages bordering padi fields. Adults were not taken in the field, and presumably play no part in malaria transmission.

Notes.

The dark legs and characteristic markings of palps and tarsi readily identify this species in the adult stage. From the rather similar *A. maculatus* both adults and larvae are distinguished by the characters discussed under that species (p. 107).

Certain variations of the Borneo specimens from the usual descriptions of this species are worthy of note. The Indian and Malayan form is shown by most authors.



as possessing a narrow pale basal band on seg. 5 of the palp, but all Borneo specimens lacked this, the dark band extending almost to the base of the segment, with a very narrow bare area proximal to it. The male terminalia also show characteristic features; the harpagones have 1-2 internal setae, a character not described for the Indian or Malayan form, and the leaflets of the phallosome appear to be more strongly serrate, the teeth extending almost to the base of some leaflets. These characters also occur in the Philippine form of this species (Russell and Baisas, 1936) and are probably correlated with some degree of geographic subspeciation. Further statistical studies may give definite evidence on this point.

Distribution.—Brunei: Brunei; Labuan Is.; Br. Nth. Borneo; Jesselton.

A. (M.) *MACULATUS* Theobald.

THEOBALD, F. V., 1901: Mono. Culic. 1, p. 171.

Type locality: Hong Kong.

Specimens examined: Four females, two males, ten larvae.

Female.

Labium (Fig. 16*b*) dark. Palps (Fig. 16*b*): seg. 2 shaggy towards base, with apical band; seg. 3 pale on apical one-third, remainder dark with a few scattered pale scales dorsally; seg. 4 pale with narrow dark band at centre; seg. 5 entirely pale; apical pale band of palp approximately equal to the subapical. Antenna with a few pale scales on seg. 2, seg. 3 with a pale tuft, and a few scattered pale scales on seg. 4.

Mesonotum dark, lighter medianly, clothed with broad flat white scales, these broadest in the fossae; a bare lateral strip posterior to each fossa, and a median bare area in front of the scutellum; anterior margin with prominent central tuft of pale hair-like scales, and smaller lateral tufts of broader scales. Pn. 1. bare or with a few scales anteriorly. Pleura dark; pr. s. absent; ust. s. and l. st. s. both 2-4; sp. s. 3-5; a few pale scales associated with sternopleural and prealar hairs.

Wing (Fig. 16*a*): Costa with prehumeral dark spot undivided or incompletely divided; apical pale spot extends along fringe to apex of vein 2-1. Vein 1 with rather long sector dark spot; central dark spot with 1-2 pale interruptions. Vein 2 with 1-2 dark spots; 2-1 with sub-basal and subapical dark spots; 2-2 with central and subapical dark spots; either or both 2-1 and 2-2 may lack one dark spot. Vein 3 with 2 dark spots near base and 1 near apex. Vein 4 pale with a few dark scales or a spot proximal to m-cu, and a long dark spot just before the fork; 4-1 and 4-2 with sub-basal and subapical dark spots or with either of these missing. Vein 5 with prominent sub-basal dark spot; 5-1 with dark spot each side of m-cu and another near apex; 5-2 with a dark spot near apex. Vein 6 with central, sub-basal and subapical dark spots. Remigium pale. Fringe pale from 2-2 to past 3, and apices of other veins; there may be a small dark interruption between 1 and 2-1, or between 2-2 and 3.

Legs: Mid coxae with scales. Femora, tibiae and tarsi 1 with white spots; may be 1 or 2 pale spots on tarsi 2 also. A variable amount of pale scaling on inside of mid and hind femora; hind femora and tibiae with narrow pale bands at apices. Fore tarsi with rather broad apical bands on segs. 1-3, smaller basal bands on segs. 2-4; seg. 4 may have a minute apical band. Mid tarsi similar to fore. Hind tarsi with broad apical bands on segs. 1 and 2, sometimes a small basal band on the latter, segs. 3-5 pale with dark band on central third, seg. 5 entirely pale.

Abdomen: Dorsal surface with a few narrow golden scales laterally towards the apex of segs. IV and V, becoming more numerous on segs. VI and VII, seg. VIII thickly

Text-figures 16-18.

Fig. 16.—*A. maculatus* Theobald. (a) Wing \times 55. (b) Palp and proboscis \times 55. (c) Harpago \times 590. (d) Leaflets of phallosome \times 970. (e) Larval head \times 120. (f) Shoulder hairs \times 290. (g) Leaflets from abdominal palmate iv \times 970.

Fig. 17.—*A. karwari* James. (a) Wing \times 55. (b) Palp and proboscis \times 55. (c) Harpago \times 590. (d) Leaflets of phallosome \times 970. (e) Leaflets from abdominal palmate iv \times 970.

Fig. 18.—*A. philippinensis* Ludlow. (a) Wing \times 55. (b) Palp and proboscis \times 55. (c) Harpago \times 570. (d) Leaflets of phallosome \times 910. (e) Hind tarsus \times 55. (f) Larval head \times 120. (g) Shoulder hairs \times 315. (h) Leaflets from abdominal palmate iv \times 570.

scaled. Ventral surface with a few dark scales near the apex of seg. VII and a few golden ones laterally on seg. VIII. Cerci with numerous dark and golden scales.

Male.

Generally similar to female. Antenna without scales on seg. 2. Venter of abdomen with a few golden scales laterally on segs. VII and VIII, the latter with a median patch of dark scales towards the posterior margin. Wing may show complete prehumeral pale spot on costa. Legs with basal banding reduced on fore and mid tarsi.

Terminalia: Phallosome bearing on each side 6-7 leaflets of decreasing size, the largest rather broad and strongly curved at the tip, with numerous serrations on distal half or entire length of concave side (Fig. 16*d*); smaller leaflets with palmate teeth at apex. Harpago (Fig. 16*c*) with club and strong apical spine, a little longer than club, and 1-3 shorter internal setae, about two-thirds length of club; apical spine may be double.

Larva.

Head (Fig. 16*e*): ic. long, rather stout, pigmented, simple with short side hairs; oc. about one-half length of ic., simple with rather stout side hairs; pc. about equal to oc., simple; sut. long, simple, rarely bifid at tip on one side; t. sut. 3-4 branched.

Shoulder hairs (Fig. 16*f*): is. with 20-24 branches; cs. with 19-24 branches; both with stout flattened stem and prominent root; os. rising very near root of cs. Pleural hairs: ppl. with 2 long simple, 1 long branched, 1 short with 3-5 branches; mpl. with 1 long simple, 1 long branched, 1 short simple or 2-3 branched, 1 minute simple; mtpl. with 2 long branched (1 with noticeably sparser branching than the other), 1 short 3-4 branched, 1 minute simple. Mt. palm. rudimentary, variable, 2-5 filamentous or flattened branches or very narrow lanceolate leaflets. Mesothoracic hair no. 1 with strong, pigmented, tapering stem and about 50 branches.

Abdominal palmate hairs (Fig. 16*f*): abd. I undeveloped with filamentous branches; abd. II developed, with lanceolate or poorly differentiated leaflets; abd. III-VII fully developed, very similar to *A. karwari*, but with tapering, fine-pointed filaments. Hair no. 5 on abd. II 5-6 branched. Lateral hair on abd. IV-VI with 3-6 branches. Psp. 5-9 branched.

Biology.

This species was rarely encountered. Small numbers of larvae were found amongst grass roots in shallow seepages, open to the sun, and in small backwaters of hillside streams, and one case was recorded of rather heavy breeding in rainwater in a wooden container. The usually low larval densities seemed to be due to the numerous predators present.

Adults were not taken in the field, but McArthur (1946) reports the northern Borneo form of this species to be highly zoophilic and a non-vector of malaria; this differs considerably from the high vector efficiency shown by the Malayan and N.E.I. forms.

Notes.

The broad banding of the hind tarsi and conspicuously spotted legs readily identify the adult of this species; *A. karwari* is somewhat similar but has dark legs. The larvae of the two species are, however, rather difficult to separate; the most reliable character seems to be the lateral hairs of abdominal segments IV-VI, which are 3-6 branched in *maculatus* and 7-12 branched in *karwari*. The fine-pointed filaments of the abdominal palmate hairs are a characteristic and easily seen feature of *maculatus*, but may become broken off to resemble *karwari*. The branching of hair no. 5 on abdominal segment II, used to separate the two species in Malaya, cannot be used for the Borneo specimens, being usually 5-6 branched in both species.

In the small series examined, no morphological characters were found which might distinguish this form from the Malayan and N.E.I. forms; the considerable difference in vector efficiency, however, seems to indicate that some degree of subspeciation has occurred. Such characters may be found if more detailed analyses are carried out,

on a larger number of specimens, as done by Christophers (1931) on the Indian forms of this species.

Distribution.—Brunei: Brunei (local report); Labuan Is.; Br. Nth. Borneo: Jesselton, Tambunan (McArthur).

A. (M.) PHILIPPINENSIS Ludlow.

LUDLOW, C. S., 1902.—*J. Amer. Med. Ass.*, 39, p. 426.

Type locality: San Jose, Luzon, Philippine Is.

Specimens examined: Forty-five females, four males, numerous larvae.

Female.

Labium (Fig. 18*b*) dark. Palps (Fig. 18*b*) rather shaggy, particularly seg. 2; segs. 2 and 3 narrowly pale at apex; seg. 4 similar but with very narrow band; seg. 5 entirely pale; segs. 3 and 4 usually with pale scales along inner surface; apical pale band of palp about equal to preapical dark band. Antenna with pale scales on segs. 2-5, those on seg. 3 forming a tuft.

Mesonotum very dark, clothed in numerous, flat, rounded, pale scales, except for a bare strip behind each fossa; anterior margin with central tuft of narrow pale scales, and lateral tufts of broader pale and dark scales. Scutellum with pale scales on posterior margin. Pn. I. without scales. Pleura dark; pr. s. absent; ust. s. and l. st. s. both 1-4; sp. s. 1-3; usually a few pale scales in the sternopleural and prealar regions.

Wing (Fig. 18*a*): Costa usually with small prehumeral, pale spot; outer third (from middle dark spot on) pale scaled on 50% or more of its length. Vein 1 with long sector dark spot, equal in length to that on costa; middle dark spot with two pale interruptions. Vein 2 with 1 or 2 dark spots; 2·1 with sub-basal and long subapical dark spots; 2·2 with dark spots at centre and towards base and apex. Vein 3 with 2 small dark spots near base and 1 subapical. On the last three veins, spotting is rather variable, and any but the subapical on 2·1 and those near the base of 3, may be missing. Vein 4 dark on distal half, except for a pale area in the region of the crossveins; 4·1 and 4·2 usually with sub-basal and subapical dark spots but variable. Vein 5 with prominent sub-basal dark spot; 5·1 with a dark spot near apex and one each side of m-cu; 5·2 with subapical dark spot. Vein 6 with 3 dark spots. Remigium pale. Fringe pale between veins 2·2 and 3 and at apices of all other veins, with a long pale area towards wing base.

Legs: Mid coxae with a tuft of pale scales, sometimes a few scales on fore coxa. Fore femora pale beneath on distal third; other femora and all tibiae and tarsi 1, largely pale beneath, with some pale scales at their apices; the latter form noticeable bands on the tibiae. Mid and hind femora with a pale patch on the outer surface near the apex, particularly conspicuous on the mid leg. Fore tarsi with pale bands at apices of segs 1-3; mid tarsi similar but with smaller bands; hind tarsi; seg. 1 with narrow pale apical band; sometimes very small; seg. 2 pale on distal 30%-50% (mean 40%); segs. 3-5 entirely pale.

Abdomen: Dorsal surface: usually a few dark scales laterally on segs. III-V; segs. VI and VII with pale scales centrally and dark scales laterally towards the apex; seg. VIII thickly scaled, mostly pale but with large dark patches laterally towards the apex, forming projecting tufts; the dark scales in a similar position on segs. III-VII also tend to form tufts. Ventral surface; seg. VII with a few broad dark scales towards the centre of the posterior margin; seg. VIII with narrow pale scales laterally and a small tuft of dark scales at the posterior lateral angles. Cerci with numerous dark scales and a few pale ones at apices.

Male.

Generally similar to female. Wing with reduced spotting on branches of veins 2 and 4. Tarsal banding reduced on fore and mid legs. Abdomen: seg. VIII with pale scales on dorsal surface, numerous dark scales on ventral surface towards the posterior margin; other segments with lateral tufts reduced or absent.

Terminalia: Phallosome with 6-9 leaflets on each side, 1 or 2 small and spine-like, the others larger, blade-like, serrated on one or both margins (Fig. 18*d*). Harpago

(Fig. 18c) very variable; club present, usually incompletely fused, with 1 or 2 subsidiary clubs or clubbed hairs; apical spine strong, slightly longer than club, occasionally doubled; usually 1-2 external spines and 1-3 internal spines, all somewhat shorter than the club; also several very small internal setae with large basal sockets.

Larva.

Head (Fig. 18f): ic. long with numerous conspicuous side hairs on the distal two-thirds, often concentrated towards the tip to give a tufted appearance; oc. about one-half length of ic., more or less dichotomously divided into numerous fine branches, giving a brush-like appearance; pc. short, divided at base into 2 or 3 (rarely 4) branches; sut. 2-4 branched; t. sut. 3-5 branched. Shoulder hairs (Fig. 18g): is. 17-23 branched; cs. 12-18 branched; both with flattened stem and rather prominent, lightly pigmented root. Pleural hairs: ppl. with 2 long simple, 1 long sparsely feathered, 1 short 3-4 branched; mpl. with 1 long sparsely branched, and 1 long, 1 short, and 1 minute, all simple; mtpl. with 2 long sparsely feathered, 1 short 2-3 branched, 1 minute simple. Mt. palm. developed with clear, pointed, lanceolate leaflets.

Abdominal palmate hairs (Fig. 18h): abd. 1 developed, leaflets lanceolate or poorly differentiated; abd. II-VII fully developed, with tapering filaments, one-half to one-third the length of the blade; pigmentation light and even in abd. I and II, darker, concentrated distally in the others. Lateral hairs of abd. IV-VI with 2-3 branches on distal half.

Biology.

Larvae of this species were found in a variety of situations, often in large numbers, usually in clear water with a fair amount of green vegetation and algae, open to the sun or lightly shaded. Favoured sites were padi fields, either with growing rice or overgrown with sedge, grassy roadside pools and drains, swamp edges, etc.

The adults could be taken in large numbers during early evening, feeding on man or water-buffalo, or resting on tent walls; in the latter case they were apparently attracted by light. The numbers caught seemed to indicate that animal blood was preferred to that of man. Dissections of 27 guts and 35 salivary glands were all negative, and there was no indication that this species plays any part in malaria transmission.

Notes.

The conspicuously pale hind tarsal segments of the adult, and the branched clypeal hairs of the larva, distinguish this species from all others known from this area. The rather similar *A. annularis* and *A. pallidus* have not yet been recorded from Borneo, except for one instance of the former from Dutch Borneo; this record is doubtful, being apparently based on a larval identification and possibly refers to the rather aberrant Borneo form of *philippinensis*. However, in the presence of these species, *A. philippinensis* adults may be distinguished by the absence of dark markings on vein 5 in the region of the fork, the presence of a pale apical band on hind tarsal segment 1, and by the rather scanty abdominal scaling. In the larval stage, identification may be difficult, but the species is reasonably well defined by the unpigmented basal tubercles of the shoulder hairs, and the relatively short filaments of the abdominal palmate hairs.

Covell (1928) has made an interesting analysis of variation in this species, and shows the existence of "local varieties", distinguished by the proportion of pale scaling on the outer third of the costa, and on the second hind tarsal segment. These ratios were highest in specimens from the Philippines (50% and 40% resp.), falling progressively to a minimum in the western Indian form (about 30% and 15.5% resp.). Corresponding ratios in the Borneo specimens examined by me were 40% (range 30%-53%) for the hind tarsus and 50% or more for the costa, i.e., identical with the Philippine specimens examined by Covell.

An examination of published descriptions shows a further distinction between eastern and western forms, in the branching of the posterior clypeal hairs of the larvae. In the Philippines, this hair is 2-4 branched (Russell and Baisas, 1934), but in the N.E.I., Malaya, and India, is 5-11 branched (Swellengrebel and Rodenwaldt

1932, Gater 1934, Christophers 1933). The N.W. Borneo specimens again coincide with the Philippine form.

In the light of modern theories of speciation, it seems that the "local varieties" of Covell (op. cit.) are best considered as geographic subspecies, arranged in an East-West cline of increasing melanism, a feature of many other animal groups, and seen also in other Anopheline species (see *A. baezi gateri* and *A. sundaicus*). Although exact definition of such subspecies may prove difficult, it seems that there are at least two distinct forms, one from N.W. Borneo and the Philippines, and one from N.E.I., Malaya, and India; these may be separated by the degree of pale scaling in the adult and the branching of the posterior clypeal hairs in the larva, the latter character being non-overlapping.

Distribution.—Brunei: Brooketon, Kuala Belait (local report); Labuan Is.; Br. Nth. Borneo: Jesselton.

A. (M.) SUNDAICUS Rodenwaldt.

RODENWALDT, E., 1926.—*Meded. Volks. Ned. Ind.*, D.1 (for. ed.), p. 87.

Type locality: Sunda Is.

Specimens examined: Twenty-two females, four males, numerous larvae.

Female.

Labium (Fig. 19*b*) dark. Palps (Fig. 19*b*) with narrow pale apical bands on segs. 2-4, seg. 5 entirely pale; pale apical band of palp about as wide as, or a little wider than, the preapical dark band. Antennae with pale scales on segs. 3 and 4. Mesonotum grey-brown, darker laterally and in the fossae; anterior margin with central tuft of narrow pale scales, lateral tufts of broad scales. Pn. I. without scales. Pleura dark without scales; pr. s. 2-4; ust. s. 3-5; l. st. s. 2-5; sp. s. 5-6. Fossae with a few broad pale scales.

Wing (Fig. 19*a*): Costa without pale interruption to prehumeral dark area; sector and presector pale spots sometimes small and bridged by dark scales on the costal margin, or rarely absent; preapical dark spot longer than pale areas adjoining it, in length 42-58% of subcostal plus preapical pale spots. Vein 1 with presector dark spot as long as, or slightly shorter than, the corresponding spot on costa; middle dark spot divided into two small spots. Vein 2 with two dark spots, and sometimes another just before the fork; 2-1 and 2-2 pale at base and apex with one or two dark spots. Vein 3 with two dark spots near base and one near apex. Vein 4 with long dark spots, one in region of the cross veins and one just before the fork; 4-1 and 4-2 pale apically and basally with two dark spots each. Vein 5 with a sub-basal dark spot; 5-1 dark near apex, and at m-cu with a few dark scales basally, dark areas totalling 42-72% of length of vein; 5-2 dark near apex. Vein 6 with central and subapical dark spots. Fringe spots present at apices of all veins, those at veins 1 and 2-1 sometimes confluent, forming one large spot.

Legs: Coxae without scales. Femora, tibiae, and tarsi 1 liberally speckled with white patches; mid and hind femora usually with much pale scaling beneath; all tibiae and hind femora with pale scales at apices. Fore tarsi with apical pale bands on segs. 1-3, narrower basal bands on segs. 2-4, seg. 5 dark; mid tarsi similar to fore, but with smaller basal bands; hind tarsi with apical bands on segs. 1-4, seg. 5 dark.

Abdomen with a few pale scales dorsally and ventrally on seg. VIII. Cerci with mixed pale and dark scales.

Male.

Generally similar to female. Antennae without scales. No ventral scaling on abdomen but numerous narrow pale scales dorsally on seg. VIII.

Terminalia: Phallosome with 7-11 leaflets each side, the larger ones blade-like or fusiform, the shortest spine-like; usually, one of the large ones with a prominent tooth near base, and sometimes some fine serrations on one of the others (Fig. 19*d*). Harpago (Fig. 19*c*) variable; usually with strong apical spine, nearly twice as long as club, and a small external spine about one-third length of club; there may be 1-2 other external or internal spines present, and the club may show subdivision.

Larva.

Head (Fig. 19e): ic. simple; oc. simple, about one-half length of ic.; pc. simple, rather long, extending past base of anterior clypeals; sut. simple or 2-3 branched; t.sut. 3-7 branched.

Shoulder hairs: is. 9-15 branched; cs. 10-14 branched; both with small root. Pleural hairs: ppl. with 2 long simple, 1 long 2-4 branched (rarely simple on one side only), 1 medium simple or bifid; mpl. with 1 long simple or 2-3 branched, 1 long, 1 short, and 1 minute, all simple; mtpl. with 2 long feathered, 1 short simple or bifid, 1 minute simple. Mesothoracic hair no. 5 with 3 branches, rarely bifid. Mt. palm. undeveloped, with 3-7 filamentous branches.

Abdominal palmate hairs (Figs. 19f): abd. I developed, leaflets lanceolate with long, elongate tips; abd. II-VII fully developed, leaflets with sharply differentiated filaments with pointed tips, narrow bases, nearly as long as blade. Psp. 5-10 branched, usually 6-8. Posterior membranous area of anal segment with numerous setae, those at level of saddle hair rather coarse, with some pigment. Lateral hairs on abd. IV-VI with 3, or rarely 2, branches from near base.

Biology.

Larvae were usually found in brackish water, not subject to tidal flushing and containing vegetation; particularly favourable were large ponds used to cultivate a floating weed which was fed to pigs. The salinity of these ponds was probably maintained by urine washed from the adjacent pig pens. All breeding sites did not conform to the above description however, and heavy larval densities were recorded on several occasions in water containing no vegetation at all; other records included breeding in a small tidal creek, and several cases from apparently fresh water. Salinities recorded ranged from 40 parts Cl_2 per 100,000 in a native well to 800 parts in a blocked tidal drain, but the usual figure was in the vicinity of 300-400 parts, i.e., one-fifth to one-sixth sea-water.

Adults were taken biting man during the early evening and, in small numbers, throughout the night, and were observed to enter houses in search of human blood. Small numbers could be found in defective mosquito nets during morning searches of native houses. No specimens were taken using animal bait, however. Dissections of 28 specimens showed all with negative salivary glands; in 21 of these, the gut also was examined and found negative.

Considering its avidity for human blood, its bad reputation from other areas, and its incrimination as a vector at Miri (Stookes 1927), it seems that this species must be looked on as a dangerous or potentially dangerous vector wherever it occurs.

Notes.

The characteristic speckled legs, normal tarsal banding, and the presence of 2 or 3 dark spots on wing vein 6, differentiate the adult of this species from others usually found in the area. However, the very similar *A. ludlowi* and *A. litoralis* have been reported from N.W. Borneo (McArthur, pers. comm.); from these species, *sundaicus* may be distinguished by the absence of a fringe spot between veins 5.2 and 6, the presence of only two dark spots on vein 1 under the middle dark spot of the costa, and the uniformly dark prehumeral area.

The larva, in common with other members of the "*ludlowi-subpictus*" group, is identified by the small, unpigmented roots of the shoulder hairs, and the sharply differentiated filaments of the abdominal palmate hairs. From the other members of this group, separation is rather difficult in some cases, particularly from *A. subpictus*. From the descriptions given by King (1932), it appears that *sundaicus* differs from *litoralis* in usually having more than three branches to the trans-sutural hair, and more than nine branches to the shoulder hairs; it also differs from *ludlowi* in the basal branching of the lateral hairs of abdominal segments IV to VI. Differences from *vagus limosus* are given under that species.

As already mentioned, the separation of larvae of *sundaicus* and *subpictus* is rather difficult, and various characters have been proposed for use in this regard. Venhuis (1938) gives a good summary of characters found by him to give an almost certain

separation of the two species in the N.E.I., but whether these hold for the Borneo forms is uncertain at present, as *subpictus* is apparently of rare occurrence in this area and no material is available for examination. Several of Venhuis' principal characters are given below; these hold for the Borneo *sundaicus*, and may possibly hold for *subpictus* also:

1. Setae lying between saddle hair and anus: coarse and pigmented in *sundaicus*, finer and unpigmented in *subpictus*.
2. Pleural hairs: all long hairs on pro- and mesothorax simple in most *subpictus*, two or more hairs branched in most *sundaicus*.
3. Postspiracular hair: usually 7 branches or more in *sundaicus*, 5 branches or less in *subpictus*.

The Borneo species is here referred to as *A. sundaicus* but in certain characters it shows an intermediate condition between the Netherlands East Indies type form and *A. litoralis*, the Philippine equivalent of this species. This was recognized by Walch and Soesilo (1929), who used specimens from Balikpapan, Borneo. They found that the ratio of dark to light scaling on the outer part of the costa (preapical dark spot/subcostal + preapical pale spots), and on vein 5·1, fell between those given by Rodenwaldt (1926) for *A. sundaicus* and *A. ludlowi*; these ratios have since been shown by King (1932) to be similar in *ludlowi* and *litoralis*. The specimens examined by me showed an intermediate condition and agreed with Walch and Soesilo's figures for the costal ratio, but were higher for the vein 5·1 ratio; this latter is rather hard to determine, however, and is much less definite than the costal ratio.

In Table 2 are set out the figures for the above ratios, together with certain other characters in which the Borneo form shows a similar intermediate condition.

TABLE 2.

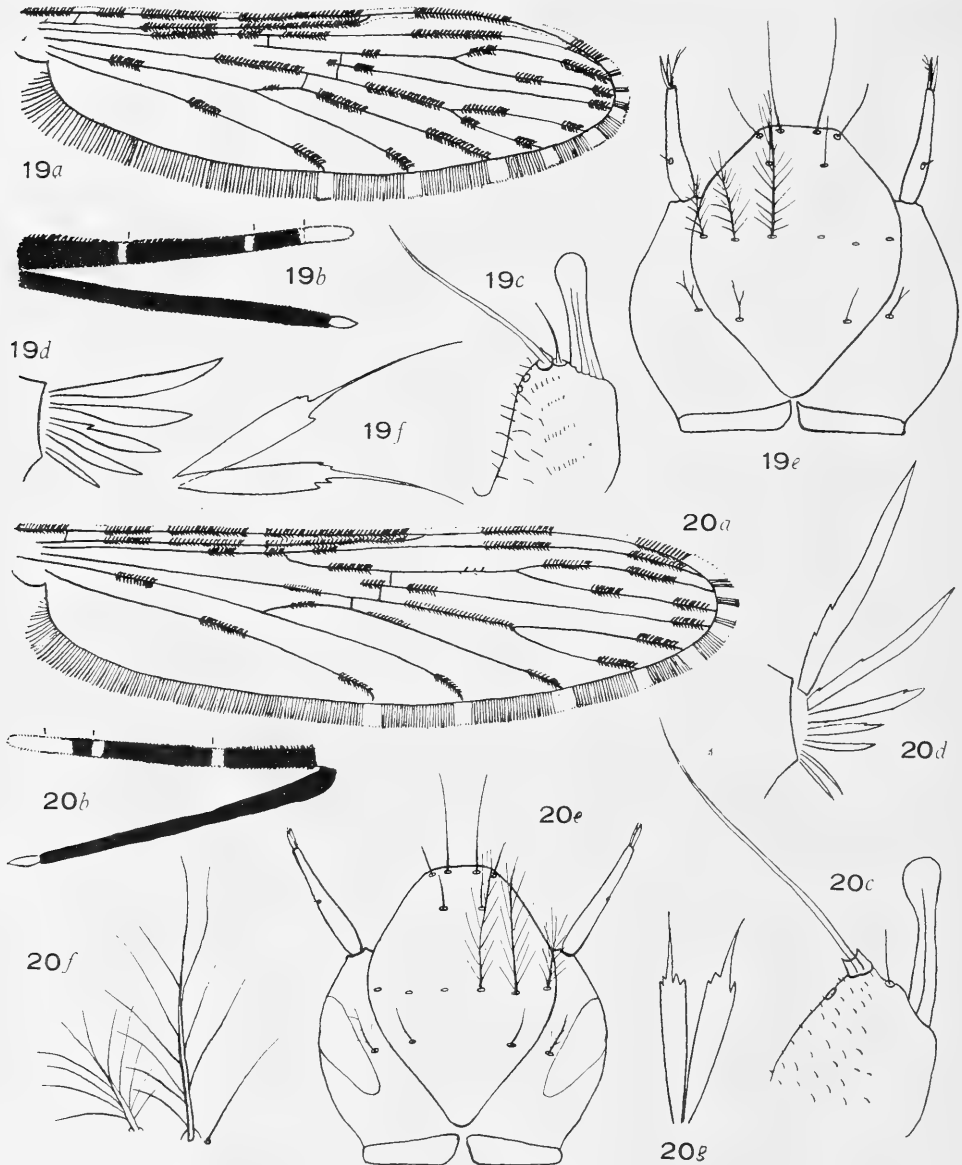
Form.	% dark/light.		% vein 2/ vein 2·2.	Sector pale costal spot.	Leaflets of phallosome.
	Costa.	5·1.			
<i>Sundaicus</i> (Rod. 1926— mixed specimens)	56·3 ±·69	63·6 ±1·04		Always present. Never bridged (Gater 1936).	Without obvious serrations (all authors).
<i>Sundaicus</i> (ibid.—total of all broods)	54·7	67·9			
<i>Sundaicus</i> (King 1932—12 specimens from Singapore)	57·0	58·0	58·0	Occasionally bridged (King 1932)	
<i>Sundaicus</i> (W. and S. 1929— Balikpapan)	47·4 ±1·3	43·0 ±1·2			One leaflet with a prominent tooth.
<i>Sundaicus</i> N.W. Borneo specimens	48·0 ±·9	52·0 ±1·8	85·0	Rarely absent, occasionally bridged.	
<i>Litoralis</i> (King 1932)	38·0	44·0	88·0	Absent in 25%, occasionally bridged.	With obvious serrations.

N.B.—Statistical analysis shows the difference between Rodenwaldt's figures for *sundaicus* and those recorded from N.W. Borneo to be highly significant (*P* less than ·01).

The systematic value of the anterior fork cell ratio used by King is rather doubtful. His figure for Singapore specimens is much lower than that indicated in descriptions and illustrations by Gater (1936).

The characters in the table above show that the Borneo form of this species differs quite significantly from the type form from the Sunda Is., and is probably worthy of subspecific rank. It also shows a connecting link between the type form and *A. litoralis*.

From the above characters, it would also appear that this last species is better considered a subspecies of *sundaicus* than a separate species, being the Philippine representative of a widespread polytypic species. *A. litoralis* is further distinguished by the presence in many specimens of a fringe spot between veins 5·2 and 6, an accessory sector pale spot on the subcosta, and pale scaling anteriorly on the prehumeral dark area of the costa. These further manifestations of hypomelanism make the Philippine form more distinct morphologically than the other two, but this is in accordance with the situation



Text-figures 19 and 20.

Fig. 19.—*A. sunndaicus* Rodenwaldt. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 570$. (d) Leaflets of phallosome $\times 910$. (e) Larval head $\times 120$. (f) Leaflets from abdominal palmate iv $\times 570$.

Fig. 20.—*A. vagus limosus* King. (a) Wing $\times 55$. (b) Palp and proboscis $\times 55$. (c) Harpago $\times 570$. (d) Leaflets of phallosome $\times 910$. (e) Larval head $\times 120$. (f) Shoulder hairs $\times 205$. (g) Leaflets from abdominal palmate iv $\times 570$.

in other animal groups, where the most outlying geographic subspecies is frequently the most distinct (Mayr, 1940, p. 167). It is interesting to note that these forms show the same arrangement of progressively paler forms as one moves from the Malayan Archipelago to the Philippine Is., as already shown in *A. baezi* and *A. philippinensis*.

It is of course possible that *A. litoralis* has become genetically, as well as geographically, isolated, and in this regard it is interesting to note that this form has been reported from N. Borneo (McArthur, pers. comm.). This may possibly refer to an extreme variation of the Borneo form, but it is also possible that *litoralis* has extended its range back from the Philippines into N. Borneo. Should it be found there meeting, but not interbreeding with, the form described above, full specific rank will have to be accorded it.

Distribution.—Brunei: Kuala Belait, Seria; Sarawak: Baram R.; Labuan Is.

A. (M.) VAGUS LIMOSUS King.

KING, W. V., 1932.—*Philipp. J. Sci.*, 47, p. 307.

Type locality: Balinatawak, Luzon, Philippine Is.

Specimens examined: Seven females, ten males, nineteen larvae.

Female.

Labium (Fig. 20*b*) dark. Palps (Fig. 20*b*): seg. 2 dark, shaggy with narrow apical pale band; seg. 3 dark with similar band; seg. 4 dark on basal third, remainder pale; seg. 5 pale; apical pale band of palp 3-4 times width of the preapical dark band and subapical pale band, which are approximately equal. Vertical pale spot rather large with scales at centre narrow and more closely appressed to the head. Antenna with a few pale scales on segs. 2 and 4 and a pale tuft on seg. 3. Mesonotum pale with dark median line, clothed in narrow, hair-like, pale scales, these broader in the fossae; anterior margin with central and lateral tufts of pale narrow scales, the latter with some dark scales laterally. Pn. 1. without scales. Pleura pale with several irregular longitudinal dark lines; pr. s. 4-5; ust. s. 3-4; 1. st. s. 4-6; sp. s. 2-3.

Wing (Fig. 20*a*): Costa with the usual six pale areas; prehumeral dark area undivided; preapical dark spot usually noticeably shorter than the pale areas adjacent to it. Vein 1 with small sector dark, spot, one-third or less the length of corresponding costal spot, frequently absent; 1 or 2 small dark spots under mid dark costal spot. Vein 2 pale with a few dark scales towards base; 2-1 and 2-2 with 1 or 2 dark spots. Vein 3 with dark spot near apex and one each side of basal crossvein. Vein 4 pale to just past crossvein r-m, then dark to the fork; sometimes a few pale scales near m-cu; 4-1 with long dark basal or sub-basal spot and a shorter subapical; 4-2 with dark subapical spot, sometimes dark basally. Vein 5 with prominent dark spot towards base; 5-1 with a dark spot each side of m-cu and one subapically; 5-2 dark near apex. Vein 6 dark at centre and near apex. Remigium pale. Fringe spots present at apices of all veins and sometimes between 5-2 and 6.

Legs: Coxae without scales. Fore femur dark towards base and apex on outer surface, remainder mixed pale and dark, but predominantly pale on distal half; other femora dark on outer surface with variable admixture of pale scaling, inner surface entirely pale except for dark subapical band on hind femur; mid femur with prominent pale subapical patch on outer surface. Tibiae pale on inner surface but hind tibia dark towards base; fore tibia dark on outer surface, others with more mixed scaling; mid tibia with narrow pale apical band; hind tibia similar but band more prominent. Fore tarsi with broad bands at the joints formed by apical pale bands on segs. 1-3, and basal bands on segs. 2-4; mid and hind tarsi similar but with much narrower bands, particularly on hind leg where basal bands on segs. 2 and 3 may be absent; hind tarsi may also show small bands at base of seg. 5 and apex of seg. 4.

Abdomen: Ventral surface with a few narrow golden scales on seg. viii and the posterior margin of seg. vii; dorsal surface with golden hairs only.

Male.

Generally similar to female. Antenna with scales on seg. 3 only. Pr. s. 2-3. Wing with middle dark spot rather long and subcostal spot shorter, relative to preapical dark

spot; presector and sector pale spots may be reduced or absent; sector dark spot on vein 1, one-half-one-third length of corresponding costal spot. Abdomen with numerous narrow pale scales on dorsum of seg. viii.

Terminalia: Phallosome bearing on each side 4-6 blade-like leaflets of decreasing size, the largest long and somewhat "S"-shaped, and 2-3 short and spine-like; most of the large leaflets with serrations along one edge (Fig. 20*d*). Harpago (Fig. 20*c*) with club and strong flattened apical spine, about twice length of club; also 1-2 shorter external spines, about one-third length of club; internal to apical spine is a sensilla resembling a spine-socket, but bearing no spine and apparently representing a vestigial internal seta.

Larva.

Head (Fig. 20*e*): ic. long simple; oc. simple, less than one-half ic.; pc. simple, a little longer than oc., placed well back, behind or slightly internal to ic.; sut. long simple or occasionally bifid; t. sut. 4-7 branched.

Shoulder hairs (Fig. 20*f*): is. with rather stout flattened stem, 12-17 branches, and medium root, widely separated from other hairs; cs. with 7-18 branches and moderately developed root. Pleural hairs: ppl. with 3 long simple and 1 medium simple; mpl. with 2 long, 1 short, and 1 minute, all simple; mtpl. with 1 long feathered, 1 long with sparse side branches, 1 short bifid or rarely simple, and 1 minute simple. Mt. palm. not developed, with 3-6 filamentous branches.

Abdominal palmate hairs (Fig. 20*g*): abd. 1 weakly developed with 3-5 flattened branches or lanceolate leaflets; abd. II-VII fully developed with well differentiated long tapering filaments, about one-half length of blade; pigment light, even. Lateral hairs on abd. IV-VI divided into 2 or 3 branches near base. Psp. 4-6 branched.

Biology.

Little can be recorded of the biology of this species as it was only taken on one occasion in a limited area near Papar, Br. Nth. Borneo. There it was found breeding in association with *A. kochi* in small open muddy pools, wheel ruts, buffalo wallows, etc., typical situations for this subspecies as recorded from the Philippines. The adults were not taken in the field.

Notes.

The adult of this subspecies may be identified as a member of the "*subpictus-vagus*" group by the form of the banding on palps and tarsi and absence of speckling on the legs. From other members of the group it is distinguished by the very broad apical pale band of the palps, the uniformly dark proboscis, and the short preapical dark spot of the costa and sector dark spot of vein 1.

The larva rather closely resembles the other members of the group *Pseudomyzomyia*. From the type form of *A. vagus*, it differs in the position of the posterior clypeal hairs; from the other species, in the short outer clypeals, the very weakly developed palmate hair on abdominal segment 1, and the unequally branched long hairs of the metathoracic pleural group. This last character, a very distinctive one in Borneo specimens at least, is not mentioned in the literature on this subspecies, but is described by Gater (1934) for the type form. Specimens of *sundaicus* and *subpictus* may show some inequality in the branching of these hairs, but to a far less degree than that described above.

This appears to be the first record of this subspecies outside the Philippine Is., but its close similarity of *A. subpictus malayensis* may have obscured its occurrence in other areas. All the specimens examined showed close agreement with the descriptions by King (1932) and Russell and Baisas (1934 and 1936) except in the shape of the leaflets of the phallosome. These are described and figured as long and straight in the Philippine form, but Borneo specimens show them as slightly longer and with a distinct "S"-shaped curvature, somewhat resembling those of *A. ludlowi*. The vestigial internal setae of the harpago are not described by the above authors but are figured by Russell and Baisas (1936). Apart from this slight difference, there appears to be no doubt as to the identity of the Borneo form with this subspecies.

Distribution.—Labuan Is.; Br. Nth. Borneo: Papar.

GENERAL BIOLOGY.

(1) LARVAL BREEDING PLACES.

The usual types of breeding place are roughly classified below, with the Anopheline species typical of such situations in N.W. Borneo.

- (i) Casual pools, buffalo wallows, etc.; light to medium shade or none; with or without vegetation; *A. barbirostris*, *hyrcanus nigerrimus*, *hyrcanus* near *sinensis*, *kochi*, *tessalatus*, *leucosphyrus* (both subspp.), *philippinensis*, *vagus limosus*.
- (ii) Seepages:
 - (a) Open to sun or lightly shaded; *kochi*, *leucosphyrus* (both subspp.), *maculatus*, *karwari*, *philippinensis*, *barbirostris*.
 - (b) Deeply shaded; *leucosphyrus balabacensis*, *aitkenii*.
- (iii) Swamps, without forest cover, but with tall grass, sedge, etc.; *barbirostris*, *hyrcanus* (both subspp.), *separatus*, sp. A near *umbrosus*, *kochi*, *philippinensis* (last two at edges only).
- (iv) Jungle and jungle fringe swamp pools; *brevipalpis*, *albotaeniatus*, *umbrosus*, sp. A near *umbrosus*.
- (v) Padi fields; *barbirostris*, *hyrcanus nigerrimus*, *kochi*, *philippinensis*.
- (vi) Tins and other artificial containers (rare); *maculatus*, *kochi*.
- (vii) Brackish water pools, usually with vegetation:
 - (a) Open to sun or lightly shaded; *sundaicus*.
 - (b) Medium to heavy shade; *baezi gateri*.

(2) ADULT HABITS.

(i) *Periods of Flight.*

Numerous observations showed that the bulk of the Anopheline population feeds during the first two hours of darkness, with maximum intensity during the first hour; for the remainder of the night, feeding is isolated and sporadic. However, information from other sources, notably unpublished data of McArthur, indicates that where *A. leucosphyrus* occurs in relatively large numbers, a peak of flight activity occurs during the first hour of the morning. Local information seemed to indicate that a similar midnight peak may occur in *A. sundaicus*.

During the day, under jungle cover, females of *A. umbrosus*, and spp. A and B near *umbrosus*, were frequently taken biting, together with an occasional specimen of *A. barbirostris* and *A. separatus*.

The following species were seen to enter houses in search of blood: *A. leucosphyrus balabacensis*, *sundaicus*, *philippinensis*, *hyrcanus nigerrimus*. None of these, however, showed any strong inclination to remain after dawn, and morning searches of native houses yielded only an occasional specimen of *A. sundaicus* trapped in a defective mosquito net.

(ii) *Blood Preferences.*

An attempt was made to determine the anthropophilic indices of the species present on Labuan Is. using the numbers caught with animal and human baits. It was soon realized that such an attempt is futile, but mathematical analysis shows that it is possible to arrange the species in a series of increasing or decreasing preference for human blood. An elementary analysis of this problem is given below.

Let x and y be the anthropophilic indices of two species, the term being used in its usual sense as the proportion of the population of that species which will normally obtain human blood. It must be remembered that this figure will only be constant for a given locality, depending to some extent on the relative opportunity of finding human or animal blood in that area. Also, let A and B be the *available* populations of the two species during the period when the catches are made with human bait, i.e., the number of mosquitoes searching for a blood feed in the area of attraction of the bait. Then during another period when catches are made with animal bait, the available populations may be represented by F_1A and F_2B , the factor F allowing for differences in the available populations during the two periods, caused by differences in actual population

density or physical factors which alter the range (or power) of attraction of the bait (amount of bait, wind, etc.). If the relative composition of the total population remains constant during the period of both catches, and if there is no interaction between the various factors combined under the "F" factor, then F_1 and F_2 will be equal.

The numbers taken in the two series of catches will then be as in Table 3.

TABLE 3.

Species.	Human bait.	Animal bait.	Ratio of human to animal bait catches. (K)
1	x_A	$FA(1-x)$	$x/F(1-x)$ (K_1)
2	y_B	$FB(1-y)$	$y/F(1-y)$ (K_2)

It can be seen from Table 3 that, since two variables are involved, the actual indices x and y cannot be derived from the catching records alone, except where they equal 0 or 1, or where the F factor equals 1. The ratio "K" can be derived, but cannot be used for direct comparison of the two species, as the ratio of their K values is not directly proportional to the ratio of the indices. However, it can be seen that if y is greater than x , K_2 is greater than K_1 , and so the species can be ranked according to their K values in a series of increasing or decreasing indices.

In Table 4 are given the figures for human and animal bait catches made over a period of several weeks on Labuan Is. Catches were all made during the same period of the evening, under roughly similar atmospheric conditions, and the F factors for the various species may be considered approximately equal. The species are arranged in order of increasing K values.

TABLE 4.

Species.	Human bait.	Animal bait.	K.
<i>kochi</i>	1	42	.024
<i>philippinensis</i>	33	91	.363
<i>barbivostris</i>	11	20	.550
<i>tessellatus</i>	3	3	1.000
<i>separatus</i>	6	1	6.000
<i>hyrcanus nigerrimus</i>	93	14	6.643
<i>leucosphyrus balabacensis</i>	11	0	Infinite

From Table 4 it can be seen that *A. leucosphyrus balabacensis* is the most avid seeker of human blood, with an infinite K value, and thus an anthropophilic index of 1 (100%), followed by the other species in the order shown. This order agrees well with that recorded from the interior of British North Borneo by McArthur (pers. comm.), but the accuracy is limited by the small numbers treated in some of the species.

The above shows that some information can be obtained from catching records as the blood preferences of the species concerned, but unless a figure can be fixed for the F factor, any results so obtained are quantitatively meaningless, and bear no relation to the index obtained by precipitin tests on mosquitoes from natural resting places. It should be noted, however, that the latter method is entirely dependent on accurate sampling of the mosquito population, and if reasonable control of the F factor could be obtained the catching method would be much simpler to use. By careful control of the various variables, it should be possible to reduce the value of F to a figure close to unity and so eliminate its influence. For instance, all catches could be made simultaneously, using a ratio of human to animal bait considered equivalent to that normally encountered by the mosquito population. Such a method would of course have to take into account all types of animal bait found favourable by the species concerned and in areas with a complex fauna of vertebrates, this may prove impossible.

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THE EMBRYOGENY OF *PHEROSPHAERA HOOKERIANA*

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(Communicated by Professor S. W. Carey.)

(Twenty-one Text-figures.)

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INTRODUCTION.

The genus *Pherosphaera*, established by Archer in 1850, consists of two species of conifers whose true relation to other forms is not yet known with any certainty and has been the subject of considerable speculation. Stiles (1912) considered that because of the morphologically erect ovules and simple strobilus and absence of an epimatium, the genus was closely related to *Phyllocladus*, which also has a simple strobilus, but in which the epimatium is symmetrical like an aril. It was not until the work of Lawson, however, that we had any knowledge of the life history. Lawson (1923) found that the three-winged pollen grains have two nuclei only, the tube and generative nuclei. Three megaspores are formed and free nuclear divisions occur in all of them, the middle one even enlarging considerably; the innermost survives. A tapetum is present. The megaspore membrane is very thin. Archegonia number three or four; their necks open laterally on the prothallus some distance from the apex. There are four neck cells. There is a shallow depression over each archegonium. A jacket layer is present. The fate of the ventral canal nucleus was not determined. The male cells were not observed, but Lawson assumed they were unequal. Lawson did not observe fertilization, nor did he describe the development of the embryo in detail. He concluded that "in the gametophyte structures and embryo of *Pherosphaera* there are no structures which justify our classifying this genus among the Podocarpaceae", to which group it had always been considered to belong. Saxton (1930), however, claimed the root nodules to be of the podocarpean type. Doyle and Looby (1939) considered that if *Pherosphaera* is a podocarp at all, it "would appear to be a very aberrant one". They pointed out the incompleteness of our knowledge, but suggested that *Pherosphaera* might provisionally be regarded as "an advanced derivative of the *Phyllocladus* line". Doyle (1945) subsequently favoured the view that it is related to *Microcachrys*.

The present investigation leads to the conclusion that *Pherosphaera* has true podocarp affinities, especially with *Dacrydium*. Lawson investigated both species, but did not distinguish between them in his account. My study of the embryo has been confined to the Tasmanian species, *P. hookeriana* Archer, which was collected on Mt. Mawson in the Mt. Field National Park. Material was fixed in formalin-acetic-alcohol, and dissection and sectioning methods were used.

In some of the material collected on 22nd March, 1947, the number of ovules per cone was counted. In 62 cones the numbers ranged from two to five, the average being 3.4. It was found that the upper two bracts were frequently sterile (Text-fig. 17, *ster. br.*), while ovules were borne in the lower bracts (*br.*). Many of these were abortive (*abort. ov.*). In 22 of the 62 cones all ovules were abortive; in 28 of them there was one fertile ovule (as Text-fig. 17); 10 had two, while only two cones had three fertile ovules. This means that 75% of the ovules were abortive. Of these, 87% had failed to develop beyond a very early stage, while the remaining ovules, which looked normal or nearly normal in size, had withered prothalli. Of the 25% with well-developed prothalli, embryos were extracted from 62% (33 ovules), of which only one had two embryo systems. These figures represent an abnormally low fertility, despite the fact that there

were plenty of both male and female plants about. The winter of 1946 was unusually severe and the season following at least three weeks late. In the same season the fertility of *Athrotaxis* was also poor.

EMBRYOGENY.

The proembryo of *Pherosphaera hookeriana* consists of a tier of six to ten prosuspensor cells and a number of embryo initials which are arranged more or less in two tiers. The lowest tier contains one or two of the units (embryo initials) and the others are in the tier above, next below the prosuspensors. In Text-fig. 3, where there are five units, the lowest tier has only one unit, while in Text-fig. 2, with the unusually large number of nine units, there are two in the lowest tier. Most proembryos have from four to six embryo units. This organization would arise in a proembryo with 16 free nuclei. One embryo system with 13-15 units was found (it was impossible to count the exact number). This presumably arose from a proembryo in which a further division to give 32 free nuclei had taken place.

The structure of the embryo units deserves attention. Some of the units are single binucleate cells, as are three of those in Text-fig. 2. Generally, however, each unit comprises two uninucleate cells. In Text-fig. 2 the large terminal embryo shows a wall running obliquely, but no sign of a wall can be seen in the plane of focus of the two nuclei, which do not appear to be separated even by a cleavage plane, nor is there any sign of persistent spindle fibres. This suggests that a wall is being laid down on a furrow which has not yet reached the centre of the cell. Looby and Doyle (1944) find that the first walls formed in the proembryo of *Podocarpus andinus* are laid down on cleavage planes, as are those terminating the binucleate state of embryo initials. In *Pherosphaera* it will be shown that walls must form by this method in slightly later stages, so that it seems certain that the walls between the two cells of two-celled units are laid down in furrows in binucleate cells. There is no definite orientation for the wall between the two cells of a unit. In Text-fig. 3 it is transverse to the axis of the suspensors in two units (only one of which is seen), parallel to that axis in two of them, and oblique in the terminal unit. Generally the shape and position of the two cells of a unit make it obvious they are sister cells. The division to form the two-celled unit takes place early, for in the smallest embryo system obtained (Text-fig. 6—its embryo units are illustrated on a larger scale in Text-fig. 1) all the units are two-celled; the second cell of the terminal unit is behind the one drawn. The embryo system from which Text-fig. 2 was taken has quite long suspensors: the development of cell walls in some units was evidently delayed.

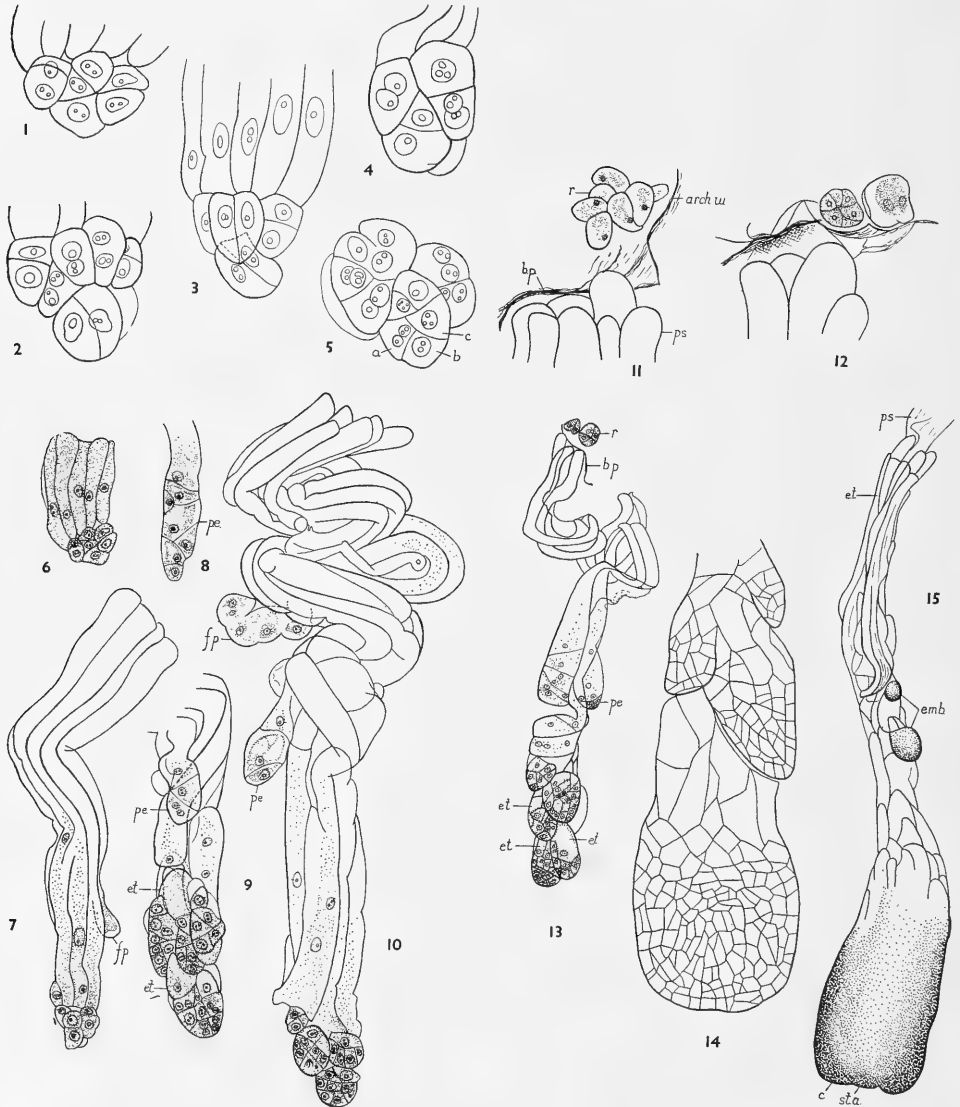
It is possible that the binucleate cells occasionally seen do not always develop into two-celled units as suggested above. One embryo unit was found with four nuclei arranged more or less tetrahedrally, with the rudiment of a wall between two of them.

During the early development of the embryo wall formation must also take place on cleavage planes after the nuclei have returned to the resting condition. Text-fig. 4 shows a condition frequently found. Two embryos are visible, one with two cells, the other with three. In the right hand embryo, the two cells of the embryo unit can be recognized. One is uninucleate; the other binucleate, the latter condition having arisen by division of the nucleus without wall formation. There is no suggestion of spindle fibres between the two nuclei. The more advanced left hand embryo has one binucleate cell, and two uninucleate, this having come about by development of a wall on a cleavage plane between the two nuclei of a binucleate cell. In Text-fig. 5 both binucleate and uninucleate cells are seen. In the terminal embryo the cells *a* and *b* are evidently sister cells. The cell *a* is binucleate; the nuclei are in a resting state, and a wall was presumably about to develop between them. The mother cell of *a* and *b* would similarly have been a sister of cell *c*, which is still uninucleate. The cells *a*, *b* and *c* are derived from one cell of a two-celled unit.

The presence of binucleate cells in young developing embryos as distinct from binucleate embryo initials has not been recorded hitherto so far as I am aware. Binucleate cells are shown in Text-fig. 9, which has embryonal tubes beginning to

elongate. Probably they do not occur in embryos older than this. In Text-fig. 10, where there are no embryonal tubes, one cell has a spindle with a wall developing on it.

As is usual, the prosuspensors elongate considerably before any further development takes place in the embryo initials (Text-fig. 7). During their elongation, prosuspensor cells are often left behind. Such a cell is indicated by *f.p.* in Text-fig. 7. In Text-fig. 10 is another in which the nucleus has divided several times, and walls are probably about to be laid down. At *pe.* in Text-fig. 10 this formation of cellular tissue has taken place. Similar conditions are illustrated in Text-figs. 9 and 13. Text-fig. 8



Text-figs. 1-15. *Pherosphaera hookeriana*. Camera lucida drawings.

Figs. 1-13 from dissected embryo systems. Fig. 14 from a section. Figs. 1-5: 22 March, 1947. $\times 275$. Figs. 6-10: 22 March, 1947. $\times 121$. Figs. 11-12: 22 March, 1947. $\times 167$. Fig. 13: 22 March, 1947. $\times 73$. Fig. 14: 21 May, 1947. $\times 133$. Fig. 15: 16 June, 1947. $\times 73$. *arch. w.*, wall of the archegonium; *b.p.*, basal plug of the archegonium; *c.*, cotyledon; *emb.*, embryo; *et.*, embryonal tubes; *f.p.*, free prosuspensor cells; *pe.*, embryos formed in prosuspensor cells; *ps.*, prosuspensor; *r.*, rosette cells; *st. a.*, stem apex.

depicts a more extensive development of cellular tissue; this figure represents the end of a single prosuspensor cell from a system with embryos similar to but larger than Text-fig. 13.

In young embryos, cells are frequently seen in the position of apical cells—e.g., Text-fig. 5 (*b*), Text-figs. 9 and 10. Some resemble the condition illustrated by Buchholz (1933*a*) for *Dacrydium*, where it is claimed that growth by the divisions of the apical cell occurs. However, I could find no evidence to enable me to state definitely whether or not apical cell growth takes place in *Pherosphaera*.

Text-figs. 9 and 13 show early stages in the development of embryonal tubes (*e.t.*), which are produced by every embryo, their growth pushing the embryos apart. Since there is an embryo in the terminal position which will become the definitive embryo, the embryogeny is of the type which Buchholz (1933*a*) calls Determinate Cleavage Polyembryony (Text-fig. 14). Where there are two embryo units in the lowest tier, the condition is perhaps somewhat indeterminate (Text-fig. 13). Embryo systems similar to Text-fig. 13 were dissected in which there were two quite large embryos on secondary suspensors of equal length. There is no primary suspensor. The prosuspensor plays no part in the separation of embryos. Although the free prosuspensor cells form "embryos", the remaining cells do not separate to carry the embryo units apart. The embryos are separated solely by the growth of the secondary suspensor.

What is properly called a rosette tier is absent in *Pherosphaera*, as in most conifers where a prosuspensor is present. Nevertheless cells are delimited above the prosuspensors, and these may divide to form groups of cells. Similar "rosette" embryos are known in many other cases, but their origin is uncertain. It has been suggested (Buchholz, 1940) that they may arise (1) by division of a prosuspensor cell at the upper end, or (2) from the relict nuclei or from the open cell tier.

In *Pherosphaera* all the "rosettes" (*r.*) are above the basal plug (*b.p.*) of the archegonium, as in Text-figs. 11–13, and hence in this case the first alternative is ruled out. Although these figures are drawn from embryo systems dissected and mounted so that the parts may be separated somewhat, in most cases the prosuspensors, basal plug and rosette cells doubtless remain in their true relative positions. There was no suggestion that cells are ever cut off from the upper end of the prosuspensors. Text-fig. 11 represents some of a group of ten cells which are probably "rosette" cells. In Text-fig. 12 one of the "rosette" embryos is binucleate; the other has six cells. Text-fig. 13 shows similar embryos with two and four cells respectively. Embryos with up to eight cells were observed. The fate of these "rosette" embryos in later stages was not determined.

The beginning of internal differentiation is seen in Text-fig. 14, which also illustrates the determinate nature of the cleavage. The terminal embryo has a large secondary suspensor and the three smaller embryos higher up each have embryonal tubes. Text-fig. 15 shows an embryo system with two small embryos (*emb.*). The terminal embryos have developing cotyledons (*c.*) between which can be seen the large stem apex (*st. a.*). The large size of the stem apex in the early stages is conspicuous. There are two cotyledons. They develop as outgrowths of the embryo, the tip of which remains round and becomes the definitive stem apex. The tip of the embryo does not flatten out and become invaginated as the cotyledons develop.

Lawson considered that the callose plug at the base of the archegonium, such as Coker (1902) described, was absent in *Pherosphaera*. Such a plug certainly was thin, and difficult to find in sections, but it could be dissected out, and is shown in Text-figs. 11, 12 and 13.

DISCUSSION.

THE PODOCARPEAN AFFINITIES OF PHEROSPHERA.

Binucleate embryo initials are regarded as characteristic of the Podocarpaceae. It has been shown by Tahara (1941) for *Podocarpus nagi*, by Looby and Doyle (1944) for *P. andinus*, and by the same authors (1939) for *Saxegothea*, that the binucleate condition arises by division of the nucleus in an original cell of the proembryo without

subsequent formation of a wall, and this is sure to be true for the whole family. In *Pherosphaera* binucleate cells occur, but more commonly the embryo units in the proembryo are two-celled. Unfortunately the material collected did not allow of a study of the development of the proembryo, but evidence suggests that the two-celled units arise from the binucleate cells by formation of walls on cleavage planes after the nuclei have returned to the resting state. Looby and Doyle (1944) show that in *Podocarpus andinus* the binucleate units give rise to four uninucleate cells by formation of walls on cleavage planes after the next division of the two nuclei, and they suggest that this process may be as characteristic of podocarps as the binucleate cells themselves. In *Pherosphaera* this process may possibly operate occasionally, but the presence of such four-celled units has not been confirmed. The usual two-celled unit in *Pherosphaera* is derived from the normal podocarp condition through the precocious development of a wall generally delayed until after the next nuclear division. This would be true both in ontogeny and phylogeny. Thus the nature of the embryo initials, binucleate and bicellular, indicates podocarpean affinities for *Pherosphaera*.

It is regrettable that Looby and Doyle have referred to the four cells formed from binucleate cells in podocarps as a *tetrad*. The use of this term ought to be confined to the four cells formed by meiosis from a spore mother cell. The terminology used in this paper is: binucleate cell; two-celled unit; four-celled unit. Embryo initials in podocarps are binucleate cells and (*Pherosphaera*) two-celled units. The two cells formed by the first division of any uninucleate embryo initial could also be designated a two-celled unit.

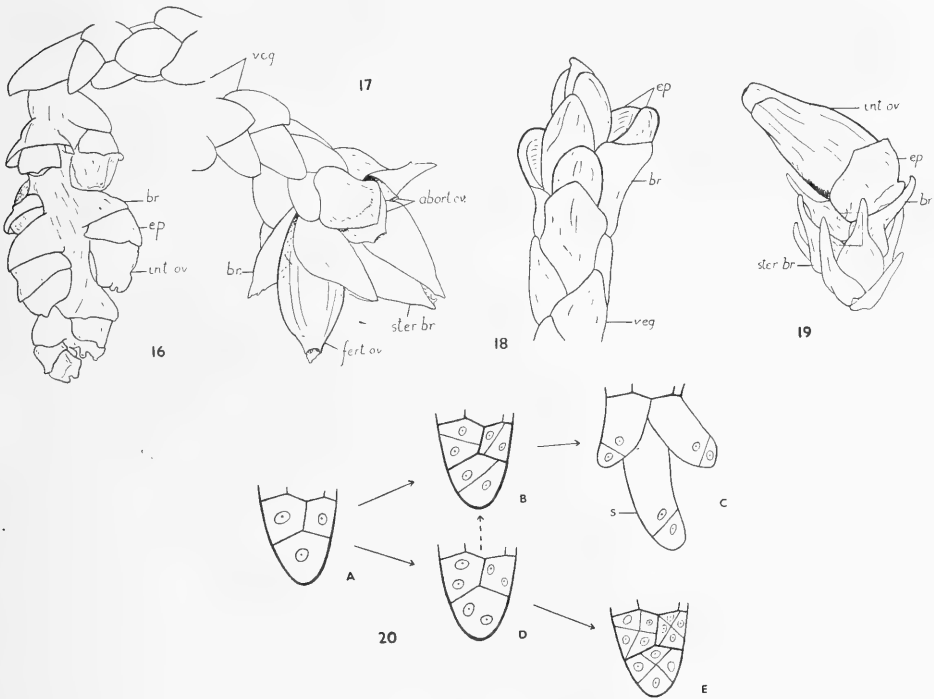
Wilde (1944) has made use of the concept of the *primary fertile branch*, a shoot which bears *fertile units* (male cones, or female shoots reduced to single ovules) in the axils of its *bracts*. She concludes (pp. 9, 34) that the primitive fertile branch had a proximal vegetative portion bearing leaves and a distal fertile portion with bracts. She shows that in the genus *Podocarpus* there are two lines of evolution. One involves reduction in the fertile branch system, large leaves being retained. In the other, the richly branched habit associated with numerous fertile branches is retained, and the leaves are reduced, being thick, keeled, imbricating and appressed to the stem. The latter group includes the sections *Dacrycarpus* and *Microcarpus*. *Dacrydium* and *Pherosphaera* both resemble the latter group, having richly branched habits and the characteristic leaf form at maturity. Their fertile branches consist of a basal vegetative portion, and a differentiated terminal fertile region in which there are generally, in the female, a number of fertile bracts (according to the species), while in the male this is represented (as in *Dacrycarpus*) by a single unit (cone).

Buchholz (1933a) studied the embryogeny of *Dacrydium cupressinum*, and described it as the type of Determinate Cleavage Polyembryony. *Pherosphaera* resembles *Dacrydium* in the arrangement of embryo units and occurrence of determinate cleavage. Buchholz's Fig. 9 (1933a) shows the terminal embryo with a long secondary suspensor while the other embryos have small embryonal tubes only. In *Pherosphaera* embryonal tubes are produced by all the embryos about the same time (see Figs. 9, 13 of this paper). In *Dacrydium* free prosuspenders forming embryos do not occur, and Buchholz did not observe "rosette" embryos.

The evidence of embryology does not support the view that *Phyllocladus* is related to *Pherosphaera*. In *Phyllocladus* the embryo units are more numerous and differently arranged, and simple polyembryony occurs (Buchholz, 1941). Moreover, the fertile branches have no vegetative portion, and the leaves are flat scales, reduced in association with the development of cladodes, and have not the keeled imbricating form as in *Dacrydium* and *Pherosphaera*.

The absence of an epimatium in *Pherosphaera* may be regarded as the culmination of an evolutionary sequence towards erectness of ovule and reduction of epimatium which is illustrated by species of *Dacrydium*. *D. bidwillii* (Text-fig. 18) has a fertile branch with two or three bracts (*br.*) subtending ovules, which are inverted at maturity, and completely enclosed by the epimatium, as in *Podocarpus*. In *D. cupressinum* (Text-fig. 19), and in *D. intermedium* and *D. colensoi*, the ovule is inverted when

young, but grows into an erect position, and the epimatium is merely a thin sheath round the base of one side of the ovule (Sinnott, 1913). The terminal portion of the fertile branch constitutes a rather definite receptacle bearing a number of sterile bracts (*ster. br.*) and a single fertile bract (*br.*). *D. franklinii* (Text-fig. 16) is more primitive in having numerous fertile bracts which are separated by considerable internodes. The axis and bracts are somewhat fleshy. It is advanced in that the ovules are erect and only partly enclosed by the epimatium. The fertile branch is strongly flexed at the base of the fertile portion, so that the micropyles still point downwards. Finally in *Pherosphaera* (Fig. 17) the vegetative part of the fertile branch is curved, making the cone pendulous, and the ovules are morphologically erect. As in *D. franklinii*, all the bracts are potentially fertile, though in the material I have examined the two uppermost bracts are frequently sterile. The axis of the cone is considerably shortened so that the bracts are crowded. There is no epimatium. As in *Dacrydium*, the nucellus is free from the integument.



Text-figures 16-20.

Fig. 16. *Decrydium franklinii*. Young female cone. $\times 7.7$. Fig. 17. *Pherosphaera hookeriana*. Female cone. $\times 10.3$. 22 March, 1947. Fig. 18. *Dacrydium bidwillii*. Young cone. $\times 7.7$. Fig. 19. *Dacrydium cupressinum*. Nearly mature cone. $\times 5.1$. *abort. ov.*, abortive ovules; *br.*, fertile bracts; *ep.*, epimatium; *fert. ov.*, fertile ovule; *int. ov.*, integument of ovule; *ster. br.*, sterile bracts; *veg.*, basal vegetative portion of fertile branch.

Fig. 20.—Diagram illustrating suggested relation between binucleate cells and primary suspensors. A-B-C represents the development in *Sciadopitys* and the Cupressineae, where uninucleate embryo initials (A) give rise to 2-celled units (B), one cell of which elongates as a primary suspensor (C/s). A-D-E represents the normal development in podocarps, where uninucleate cells (A) give rise to binucleate cells (D), which in turn give rise to 4-celled units (E). The arrow D-B points to the homology between binucleate cells and 2-celled units, and also illustrates the mode of formation of 2-celled units from binucleate cells in *Pherosphaera*.

Unfortunately it is not possible at present to institute detailed comparisons between the gametophytic structures of *Dacrydium* and *Pherosphaera*. Our knowledge of the morphology of *Dacrydium* is due chiefly to the work of Young (1907), who described the male gametophyte, of Stiles (1911), who described the mature female gametophyte

and the male gametes, which are unequal, and of Sinnott (1913), who gave an outline of the development of the gametophytes and embryo. Buchholz (1933a) has described the embryo. It would appear that *Pherosphaera* differs chiefly in the absence of male prothallial cells; in the position of the archegonia, and the fact that they are not deeply buried by the growth of prothallial tissue; in the thickness of the megaspore membrane, and in the presence of two-celled embryo units. It is difficult to estimate the significance of these features. The accounts of development in both genera are lacking in many details—such as the formation of gametes, and fertilization—which would be invaluable for comparison. A detailed study of the development of *Dacrydium* is urgently needed, and more details of *Pherosphaera* are required. In view of the considerable differences in cone structure manifest in the different species of *Dacrydium*, investigation of several species might be desirable. Nevertheless, while Lawson considered that the gametophytic structures of *Pherosphaera* do not justify our classifying it with the Podocarpaceae, there are no such structures which cannot be regarded as derived from those of more typical podocarps.

THE TAXONOMIC STATUS OF PHEROSPHAERA.

Pilger (1926) divided the Podocarpaceae into three subfamilies: Pherosphaeroideae, containing only *Pherosphaera*; Podocarpoideae, including *Microcachrys*, *Saxegothea*, *Dacrydium*, *Acmopyle* and *Podocarpus*; and Phyllocladoideae, with *Phyllocladus*. More recently Buchholz (1933b) has proposed a family Pherosphaeraceae, containing the one genus *Pherosphaera*.

Although *Pherosphaera* has some characters which are very different from those of other podocarps, a case has been made out for regarding it as developed from *Dacrydium*-like forms. If our classification is to reflect phylogenetic relationships, *Pherosphaera* should be placed in the same group as *Dacrydium*, and not in a group of equal independent status.

The greatest similarity between *Dacrydium* and *Pherosphaera* lies in the nature of cone and fertile branch. The organization of the fertile branch in these two genera is essentially similar to that originally described by Wilde (1944) for *Dacrycarpus* and *Microcarpus*. The same type of organization can be shown to occur in *Microcachrys*, which has a fertile branch with a proximal portion which is vegetative, having small keeled imbricating leaves arranged in four ranks, and a distal fertile portion in which the bracts are spirally arranged and form a definite cone. The bracts become very fleshy. *Acmopyle* would also appear to have a fertile branch in which the basal part is vegetative and bears small leaves.

Thus the nature of the primary fertile branch seems to provide the basis for a natural scheme of classification, and I therefore suggest that one subfamily of the Podocarpaceae should include *Dacrydium*, *Pherosphaera*, *Microcachrys*, *Acmopyle*, and possibly the genus proposed by Wilde, comprising the present *Dacrycarpus* and *Microcarpus* sections of *Podocarpus* together with *Podocarpus vitiensis* and *P. minor*. The subfamily could be called the *Dacrydioideae*. It would be characterized by the richly branched habit associated with retention of the complete fertile branch system; and by the fertile branches having a well-developed basal vegetative portion in which the leaves are typically keeled and imbricating.

The validity of this proposed grouping is a matter which should be investigated further. In particular, the position of the *Podocarpus* spp. should be examined. The receptacle of *Dacrycarpus* is composed of the fleshy bases of the bracts (Gibbs, 1912), and the lamina of the fertile bract is fused to the epimatium of the ovule. Thus the receptacle is not entirely homologous with that of *Eupodocarpus*, and it is conceivable that it evolved independently.

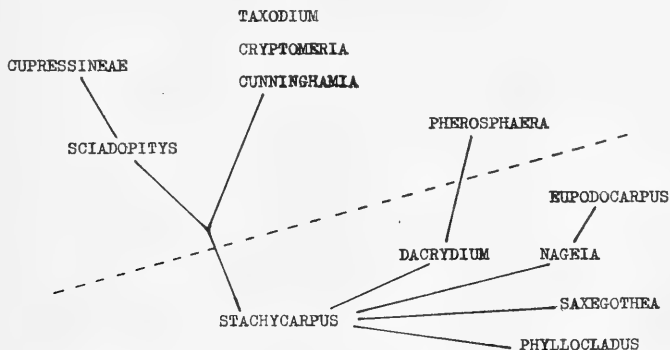
This proposed group of genera with fertile branches in which the basal vegetative part is well developed is to be contrasted with other podocarps in which the fertile branch is reduced, or in which the basal vegetative portion is not well developed. Even if the species at present placed in *Podocarpus* be not included, *Dacrydium*, *Pherosphaera*

and *Microcachrys* at least constitute a natural group, which, if diverse in some respects, is closely united on the basis of cone and fertile branch morphology.

BINUCLEATE CELLS AND PRIMARY SUSPENSORS.

The most distinctive feature of the embryogeny of *Pherosphaera* is the usual occurrence of two-celled embryo initials instead of the binucleate cells which are general for the Podocarpaceae. The genus will therefore be important in any discussion on the significance of these binucleate cells. When the two cells in *Pherosphaera* are superposed, they recall the corresponding stages in conifers such as *Chamaecyparis* and *Biota* (Buchholz, 1932a), and *Sciadopitys* (Buchholz, 1931), in which the upper cell of a two-celled unit elongates as a primary suspensor. In the case of *Sciadopitys*, Buchholz states (p. 260) that "the small embryos are variously oriented and begin to elongate in all directions", corresponding to the haphazard direction of the wall in the two-celled unit of *Pherosphaera* as noted above. It may be then that the absence of a primary suspensor in Podocarpaceae is correlated with the occurrence of binucleate cells dividing into four-celled units, the two courses being mutually exclusive (Text-fig. 20). The condition seen in *Pherosphaera* is probably not primitive for the family, but derived, as are its other peculiarities, e.g., absence of male cells and of epimatium, reduced megaspore memberane (Lawson, 1923).

Buchholz (1931) regards the embryogeny of *Sciadopitys* as a type from which those of the Cupressineae and Taxodiaceae may have been derived, and he points out also the resemblance, "at least in general organization", to *Podocarpus spicatus*, a member of the *Stachycarpus* group. The proembryo of *Sciadopitys* was described briefly by Lawson (1910). Wall formation takes place with sixteen free nuclei. Below the prosuspensor tier is a single tier of cells which "divide repeatedly," forming three or four rows which taper to a point" (p. 416). The cells of these tiers are the embryo initials. In *Podocarpus andinus* (Looby and Doyle, 1944), on the other hand, a similar final arrangement arises by a different process. There are thirty-two free nuclei, at the base of the archegonium, and walls develop on cleavage planes giving rise directly to the cells which become embryo initials. If the presence of binucleate cells in developing embryos as in *Pherosphaera* is demonstrated in more typical species, it would indicate a tendency in podocarps to delay wall formation unrelated to primary suspensor formation. In *Podocarpus dacrydioides* and *P. totara*, Buchholz (1941) figures spindle fibres between the two nuclei of the binucleate cell. Thus it would appear that in the more advanced podocarps wall formation on cleavage planes, probably related to the delay in their formation, is being eliminated. I suggest that the two different ways in which a comparable final proembryo is achieved in *Stachycarpus* and *Sciadopitys* result from this variation in the time at which walls are laid down. The two-celled embryo initials being a derived state in *Pherosphaera*, we can postulate that the presence of two-celled units in *Sciadopitys* and elsewhere is similarly an advanced condition.



Text-fig. 21.—Suggested relationships between different types of embryology in the Podocarpaceae and Taxodiaceae. The genera above the broken line possess two-celled units.

In *Pherosphaera* both cells of the two-celled unit contribute to a single embryo, and this is true also of *Cunninghamia*, *Cryptomeria* and *Taxodium* (Buchholz, 1932b, 1940; Coker, 1903), which have no primary suspensors. In the evolution of *Sciadopitys*, however, it is suggested that one of the cells of the two-celled unit became the primary suspensor, and the definitive embryo grew from the other cell (Text-fig. 21).

SUMMARY.

In the proembryo of *Pherosphaera hookeriana* there are six to ten prosuspensor cells and generally four to six embryo initials arranged in two tiers. Embryo initials are binucleate cells or, more usually, two-celled units of two uninucleate sister cells. The two-celled units are formed from the binucleate cells by a wall laid down on a cleavage plane. Formation of four-celled units direct from the binucleate cells possibly also occurs. Binucleate cells also occur in embryos during early stages of their growth. Each embryo develops independently and produces embryonal tubes, by the growth of which the embryos are separated. The type of cleavage is determinate. Abnormal embryos are produced in the free prosuspensor cells, and "rosette" embryos occur sporadically.

It is contended that the nature of the embryo initials indicates podocarpean affinities, since the walls dividing the two cells of the two-celled units represent a precocious development of the walls generally delayed until after the two nuclei of the binucleate cells have divided again. The embryogeny otherwise resembles that of *Dacrydium*, and the absence of an epimatium can be related to an evolutionary sequence illustrated in *Dacrydium* species. *Pherosphaera* has a richly branched habit and small keeled imbricating leaves. Its systematic position lies in a subfamily of the Podocarpaceae, including also *Dacrydium* and *Microcachrys*, with possibly *Acmopyle*, and the *Dacrycarpus* and *Microcarpus* sections of *Podocarpus*. In these the fertile branches have a well-developed basal vegetative portion.

It is suggested that one cell of the two-celled embryo unit represents the cell which elongates to form the primary suspensor in some conifers, and absence of this structure in podocarps is correlated with the presence of binucleate cells.

ACKNOWLEDGEMENTS.

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THE ORCHID FLORA OF THE CENTRAL WESTERN SLOPES OF
NEW SOUTH WALES.

By the REV. H. M. R. RUPP, B.A.

(Two Text-figures.)

[Read 30th June, 1948.]

In these PROCEEDINGS, Second Series, Vol. I (1886), 867, the late A. G. Hamilton, then a school teacher at Guntawang, near Mudgee, published a census of the Orchids of the Mudgee District; and in the following year (*ibid.*, 1887: 865), he made a further contribution to the botanical knowledge of that area in the form of a census of the general flora of Mudgee. In this a few more orchids were added, bringing the total number of species enumerated up to sixty-two.

These valuable papers of Hamilton's appear to have been completely forgotten and lost sight of after the author's death. I have been trying for some years to ascertain whether any account of the orchid flora of the Central Western Slopes had ever been published, but with no success. From 1945 to 1947 the brothers G. W. and P. Althofer, of Dripstone, near Wellington, had been diligently searching over a large area of the Slopes, with a view to recording its orchids. In the *Victorian Naturalist* for August, 1946, G. W. Althofer published a list of the species they had found up to date, and it was generally assumed in orchidological circles that this was the first record to be made public. Knowing what a keen and capable botanist A. G. Hamilton had been, and often having heard him speak with enthusiasm of the Guntawang flora, I found it difficult to believe that he had never published the results of his botanical excursions there. Accordingly I recently began a search among old volumes of these PROCEEDINGS, and was pleased to find the two papers cited above.

Althofer's list records 45 species of orchids, including six which he and his brother had not collected themselves. Hamilton's list of 62 includes several which he had not seen personally, but their records had been given to him by Dr. Woolls, who had done some botanical collecting around Mudgee.

A few species from the Central Western Slopes not recorded by either Hamilton or Althofer are represented in the National Herbarium at Sydney. If we add to these the three new species of *Diuris* described in the present paper, the grand total of species actually recorded for the Central Western Slopes is now 83. Before giving the list, however, it may be advisable to indicate what is meant here by "Central Western Slopes". A line drawn eastward from Dubbo through Gulgong would meet the Main Dividing Range a few miles beyond the latter town; and this line may be taken as the northern boundary of the area concerned; while the southern boundary would be the Lachlan River. The western side of the Main Divide, from Gulgong through Portland and Oberon to the Abercrombie River, would be the eastern boundary. The western boundary would begin wherever the Slopes pass into the Western Plains. The south-east corner of this area, towards the Abercrombie River, was not visited by either Hamilton or the Althofer brothers (see Text-fig. 1).

Hamilton's list contains some names which are obsolete; in the list given below I have simply altered these to the names now recognized as valid. In one instance I have ventured to substitute a specific for a varietal name. He records a variety of *Prasophyllum patens* which is not now accepted; it is, I am confident, identical with *P. odoratum* Rogers, which has been sent in by the Althofer brothers from the same district. He also records *P. alpinum* R. Br. As this species is restricted to high alpine localities, obviously a mistake had been made; and it is, I think, explained by the fact

that R. D. Fitzgerald, who identified most of Hamilton's specimens, wrongly interpreted the species. His figure in *Austr. Orch.* II, 1, over the name *P. alpinum*, is certainly not Brown's species, but represents the plant named by Rogers *P. gracile*, which has also been sent in by the Althofers.

ORCHIDS OF THE CENTRAL WESTERN SLOPES.

THELYMITRA	<i>ixioides</i> Sw. *	CALADENIA	<i>Fitzgeraldii</i> Rupp. A.
"	<i>longifolia</i> Forst. H.	"	<i>Patersonii</i> R. Br. A.
"	<i>aristata</i> Lindl. H., A.	"	<i>arenaria</i> Fitzg. H.
"	<i>nuda</i> , R. Br. H., A.	"	<i>dilatata</i> R. Br. H., A.
DIURIS	<i>punctata</i> Sm. H. *	"	<i>clavigera</i> Cunn. A.
"	<i>Colemanae</i> Rupp. *	"	<i>filamentosa</i> R. Br. H., A.
"	<i>Sheaffiana</i> Fitzg. **	"	<i>carnea</i> R. Br. H., A.
"	<i>tricolor</i> Fitzg. H., A.	"	<i>congesta</i> R. Br. ***
"	<i>maculata</i> Sm. H., A.	"	<i>alba</i> R. Br. H.
"	<i>brevissima</i> Fitzg.-Nich. A.	"	<i>dimorpha</i> Fitzg. A. ***
"	<i>flavopurpurea</i> Messm. A.	"	<i>angustata</i> Lindl. A.
"	<i>lineata</i> Messm. A.	"	<i>cucullata</i> Fitzg. H., A.
"	<i>polymorpha</i> Messm. A.	"	<i>deformis</i> R. Br. +
"	<i>Althoferi</i> Rupp, n. sp. A.	"	<i>caerulea</i> R. Br. H., A.
"	<i>cucullata</i> Rupp, n. sp. A.	GLOSSODIA	<i>major</i> R. Br. H., A.
"	<i>cuneilabris</i> Rupp, n. sp. A.	CORYBAS	<i>diemenicus</i> (Lindl.), H. ++
"	<i>dendrobioides</i> Fitzg. H.	PTEROSTYLIS	<i>concinna</i> R. Br. H.
"	<i>striata</i> Rupp. **	"	<i>curta</i> R. Br. H., A.
"	<i>platichila</i> Fitzg. A.	"	<i>nutans</i> R. Br. H., A.
"	<i>palachila</i> Rogers. A. ***	"	<i>acuminata</i> R. Br. H.
"	<i>sulphurea</i> R. Br. H., A.	"	<i>clavigera</i> Fitzg. H.
"	<i>aurea</i> Sm. H., A.	"	<i>revoluta</i> R. Br. H., A.
"	<i>abbreviata</i> F. Muell. H. *	"	<i>reflexa</i> R. Br. H.
"	<i>pedunculata</i> R. Br. H.	"	<i>alata</i> Lindl. H.
MICROTIS	<i>unifolia</i> (Forst.) Rchb. f. H., A.	"	<i>obtusa</i> R. Br. H.
"	<i>parviflora</i> R. Br. H., A.	"	<i>parviflora</i> R. Br. H., A.
PRASOPHYLLUM	<i>elatum</i> R. Br. H.	"	<i>Woolsii</i> Fitzg. H., A.
"	<i>flavum</i> R. Br. H.	"	<i>rufa</i> R. Br. H., A.
"	<i>gracile</i> Rog. H., A.	"	<i>squamata</i> R. Br. H.
"	<i>brevilabre</i> Hk. f. H.	"	<i>Boormanii</i> Rupp. A.*
"	<i>odoratum</i> Rog. H., A.	"	<i>Mitchellii</i> Lindl. H.
"	<i>patens</i> R. Br. H., A.	"	<i>mulica</i> R. Br. H., A.
"	<i>fuscum</i> R. Br. H.	"	<i>cycnocephala</i> Fitzg. H.
"	<i>rufum</i> R. Br. H.	SPIRANTHES	<i>sinensis</i> (Pers.) Ames. *
CALEANA	<i>minor</i> R. Br. H., A.	LIPARIS	<i>reflexa</i> Lindl. H.
CHILOGLOTTIS	<i>formicifera</i> Fitzg. H., A.	DENDROBIUM	<i>speciosum</i> Sm. H.
"	<i>trapeziformis</i> Fitzg. H.	"	<i>teretifolium</i> R. Br. H.
ACIANTHUS	<i>formicatus</i> R. Br. H., A.	DIPODIUM	<i>punctatum</i> R. Br. H.
"	<i>reniformis</i> (R. Br.) Schltr. H., A.	"	<i>Hamiltonianum</i> Bail. A.
CALOCHILUS	<i>campestris</i> R. Br. H., A.	CYMBIDIUM	<i>suave</i> R. Br. H.
"	<i>Robertsonii</i> Benth. A.		
ERIOCHILUS	<i>cucullata</i> (Lab.) Rchb. f. H., A.		
LYPERANTHUS	<i>suaveolens</i> R. Br. H.		

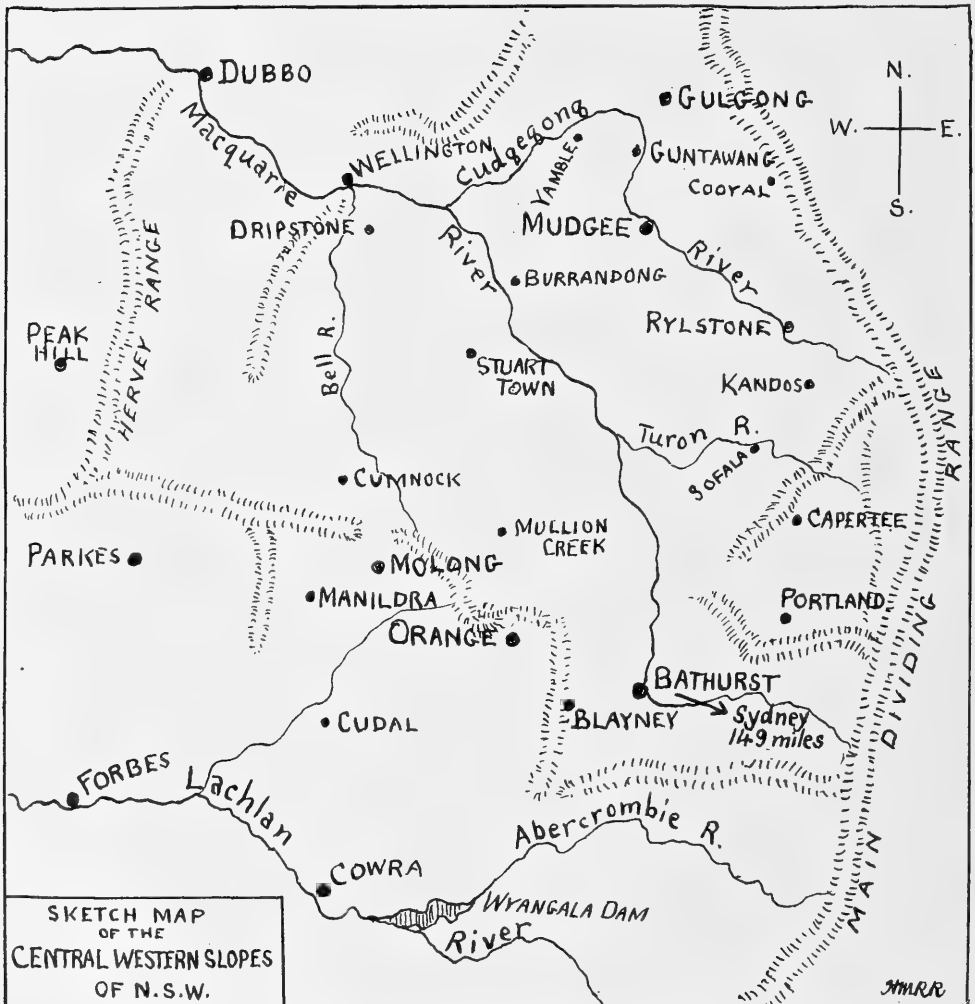
In the above list the letter H. after a species signifies that it was recorded by Hamilton. The letter A. stands after the species collected by the Althofer brothers. A single asterisk after a species indicates that the collector was J. L. Boorman; two asterisks, that the collector was G. H. Sheaffe; three, that the collector was W. F. Blakely. Boorman's and Blakely's specimens are in the National Herbarium at Sydney; Sheaffe's are recorded by R. D. Fitzgerald.

The sign +: *Caladenia deformis* was collected by the present writer at Molong, 9.1916.

The sign ++: *Corybas diemenicus* was found by Hamilton near Guntawang in 1886. Being unaware of its identity, he sent it to R. D. Fitzgerald, who considered it an undescribed species, and proposed to name it *Corysanthes Hamiltonii*. (The genus *Corybas* was then known as *Corysanthes*.) It is figured in one of his unpublished plates in the Mitchell Library at Sydney, but never reached publication. Hamilton sent admirable specimens to the Sydney and Melbourne Herbaria. W. H. Nicholls and the present writer, after carefully examining these specimens and Fitzgerald's plate, determined the plant as Lindley's *Corysanthes diemenica*. (See these PROCEEDINGS, liii, 1928, 86.) In 1945 a living specimen in flower was sent to the Naturalists' Society of N.S.W. from Mullion Creek, between Orange and Dripstone. It was referred to me for determination, and it was found to be a typical *Corybas diemenicus*. It is curious that the Guntawang and Mullion Creek records, from the Central Western Slopes, are the only New South Wales records of this little Helmet Orchid, which is quite common near the coast in the southern States.

The most arresting feature of the list given above is the remarkable number of species of the genus *Diuris* (20). The development of so many strikingly different forms of this genus within New South Wales is extraordinary. Including the three new species which are described in this paper, the number now recognized for this State is 31. The numbers for the other States are: Queensland, 11; Victoria, 10; South Australia, 8; Western Australia, 7; and Tasmania, 6. Even if it should ultimately be established that (as has been suggested) a few of the recognized New South Wales species are no more than extreme variations from the type forms of previously described species (a suggestion which I am unable to endorse), such a conclusion would not materially affect the disproportionate development of the genus in New South Wales.

In 1945 and 1947 more than 40 different forms of *Diuris* were sent to me by the Althofer brothers from the Central Western Slopes. After studying these very carefully and comparing them critically with the numerous species now represented in the National Herbarium of New South Wales, I am unable to reconcile a number of them with any of the known species. By making allowance for variations not mentioned in any published descriptions, I have placed some in *D. maculata*, *D. palachila*, *D. tricolor*, *D. flavopurpurea*, and *D. lineata*. The three new species, *D. Althoferi*, *D. cucullata*, and



Text-fig. 1.—Locality map of the Central Western Slopes of New South Wales.

D. cuneilabris, seem to be well established, and to be irreconcilable with existing species without expanding the descriptions of the latter to such an extent as to make identification very difficult. A form collected near Dubbo at first glance resembling *D. longifolia* R. Br., with the same beautiful blend of brown and yellow, appeared to be a new species; but subsequently, closely allied forms from other parts of the area proved so perplexing that I have preferred to let this group stand over in the hope of additional living material being collected next season. Some of the forms received strongly suggest natural hybridization between the following; *D. lineata* × *D. flavopurpurea*; *D. maculata* × *D. flavopurpurea*; *D. palachila* × *D. lineata*; *D. platichila* × *D. lineata*.

I desire here to offer some remarks upon the "raised lines" or longitudinal ridges on the disc of the labellum which are found in the great majority of species of *Diuris*. They have been largely used in descriptions as distinguishing features, according to their number, one, two, or three. They appear to be glandular structures, and are probably instrumental in guiding insect visitors to the column for purposes of pollination. In a personal communication from the Victorian orchidologist, W. H. Nicholls, he alludes to them as "callous plates", and in my opinion this term is much to be preferred to "ridges" or "raised lines", and is more truly descriptive. My observations have led me to believe that there are *never more than two* of these structures. When there appear to be three, it will be found, if a careful examination be made, that the middle one is very different from the two laterals, and, in fact, is merely a longitudinal raising of the surface of the disc. It might well be termed a *keel*, and is often directly continued as such along the middle line of the mid-lobe. When the labellum is pressed and dried, this median "ridge" almost completely disappears, while the lateral pair remain very distinct. In some species it is not present even in the living flower. In such species as *D. longifolia* and *D. sulphurea* there are no callous plates at all, but only a single longitudinal raising of the discal surface. I think therefore that a distinction should be made between the glandular longitudinal *callous plates* and the *discal keel*, which in some species lies in between them.

DESCRIPTION OF NEW SPECIES OF DIURIS.

D. ALTHOFERI, sp. nov.

Planta gracilis, usque ad 35 cm. alta. Folia 2-3, linearia, c. 22 cm. longa. Flores 3-7 in racemum flexuosum, pallide flavi. Sepalum dorsale c. 1 cm. longum, erectum marginibus reflexis et apice obtusissimo. Sepala lateralia fuscoviridia, 16-20 mm. longa, saepe transversa, prope apices dilatata. Petala patentia, non maculata; lamina ovata, c. 12-13 mm. longa, in ungue brevi et fusco. Labellum 12-13 mm. longum, trilobatum; lobi laterales 5-6 mm. longi, patentis, reflexi, obtusi vel breviter acuti, marginibus superioribus crenulatis vel denticulatis. Lobus intermedius disco brevi; bractee callosae 2, a carina humili disjunctae; lamina orbicularis vel raro late ovata, non maculata vel raro 2-3 maculis fuscis. Columnae alae a fronte obscurae, fere triangulares, paululum denticulatae, humiliores quam anthera.

A slender plant not exceeding 35 cm. in height. Leaves 2 or 3, about 22 cm. long, a little broader than in other species of similar dimensions. Flowers 3-7 in a flexuose raceme, clear lemon yellow. Dorsal sepal about 1 cm. long, more or less erect, with a large dusky forked blotch near the base; margins reflexed, apex very obtuse. Lateral sepals narrow but slightly dilated towards the apex, green and brown, 16-20 mm. long, often crossed. Petals spreading, neither spotted nor blotched, the lamina ovate, about 12-13 mm. long, on a dark claw 4-6 mm. long. Labellum about as long as the lamina of the petal or a little shorter, trilobate, lateral lobes almost lanceolate, about half as long as the mid-lobe, obtuse or shortly acute, spreading and sometimes reflexed, upper margins minutely crenulate or denticulate. Mid-lobe with a rather short disc; callous plates separated by a low keel; lamina most frequently orbicular, but sometimes broadly ovate, neither spotted nor blotched, or occasionally with 2 or 3 short brownish markings above. Wings of the column obscure from the front, nearly triangular, slightly denticulate, not as high as the anther.

Guntawang and Yamble Mountain, 9.1947 and 10.1947, G. W. and P. Althofer.

A dainty and attractive species, perhaps most nearly allied to *D. platichila* Fitzg., but quite distinct. The specific name is a tribute to the valuable work of the Althofer brothers in connection with the orchid flora of the Central Western Slopes.

D. CUCULLATA, sp. nov.

Planta gracillima, usque ad 30 cm. alta. Folia 2, angustissime linearia, c. 25 cm. longa. Flores pauci, sulfurei maculis fuscopurpureis. Sepalum dorsale a basi horizontale, ad apicem plus minusve cucullatum, acutum, c. 1 cm. longum. Sepala lateralia fuscoviridia, usque ad 15 mm. longa, gracillima, aliquando transversa. Petala patentia, divaricatissima, non maculata; lamina ovato-acuta, fere 1 cm. longa, in ungue fusco 5-6 mm. longo. Labellum c. 12 mm. longum, trilobum; lobi laterales c. 7 mm. longi, angusti, breviter acuti, maculis paucis, marginibus superioribus denticulatis. Lobus intermedius disco longo et angusto, non carinato; bracteae callosae 2. Lamina comparate parva, spatulata vel fere orbicularis, supra conspicue carinata, infra magnopere maculata. Columnae alae a fronte conspicuae, paululum altiores quam anthera, dentatae.

A very slender plant up to about 30 cm. high. Leaves in my specimens 2, very narrow-linear, about 25 cm. long. Flowers few, sulphur-yellow with purplish-brown markings. Dorsal sepal apparently never erect, horizontal from the base, towards the apex deflexed (cucullate), acute, about 1 cm. long. Lateral sepals brown and green, up to 15 mm. long, very slender, sometimes crossed. Petals spreading, very divergent, not spotted; lamina ovate-acute, nearly 1 cm. long, on a brownish claw 5-6 mm. long. Labellum about 12 mm. long, trilobate; lateral lobes rather more than half as long as the mid-lobe, narrow, shortly acute, slightly spotted, upper margins denticulate. Mid-lobe with a long narrow disc, not keeled, callous plates very slender; lamina rather small, nearly orbicular or somewhat spatulate, conspicuously keeled above, usually heavily spotted or blotched below. Wings of the column conspicuous from the front, a little higher than the anther; dentate.

Gulgong, 10.1945, and Yamble, near Guntawang, 9.1947; G. W. and P. Althofer.

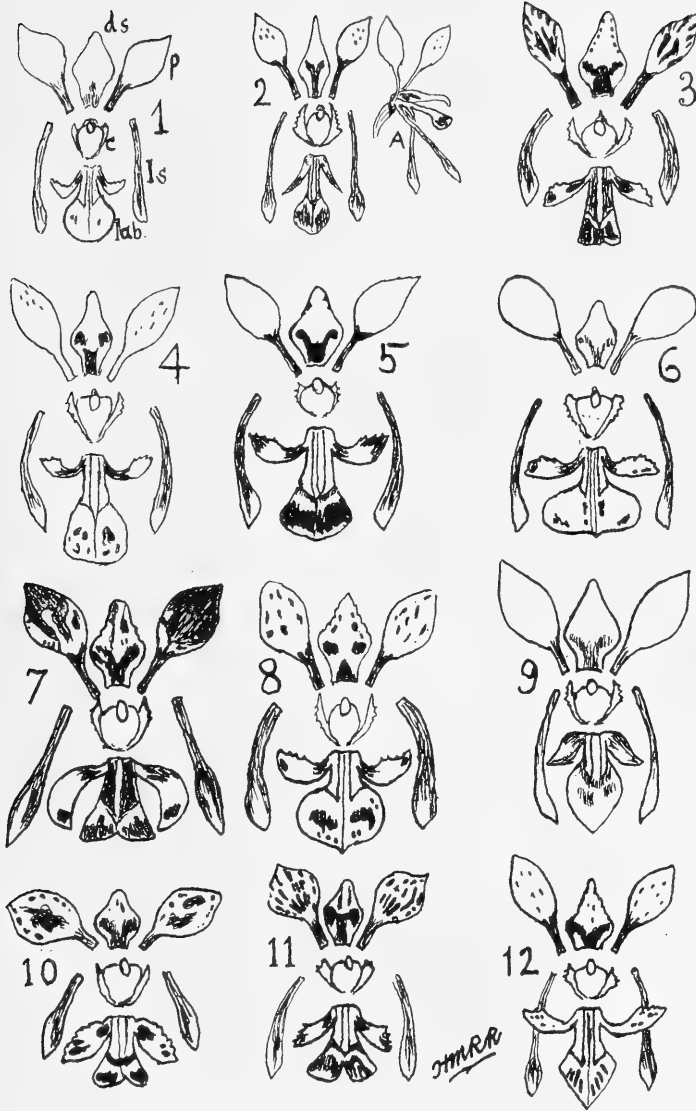
A peculiar form, apparently rare, but collected in two different areas. In every flower seen, the dorsal sepal was horizontal, deflexed towards the apex; this unique character suggested the name *cucullata*, although strictly speaking the segment is not curved and "hooded" as in various species of *Caladenia*. The contour of the labellum is also unique, resembling that of a Roman vase or flask (*ampulla*).

D. CUNEILABRIS, sp. nov.

Planta moderate robusta, usque ad 60 cm. alta. Folia 2, linearia, 25-35 cm. longa. Bracteae floreae abrupte acutae. Flores nonnulli, fulvi notationibus fuscis, aliquantum magni. Sepalum dorsale erectum, fere rhomboideum, ad basim magnopere signatum, ad margines anteriores maculatum. Sepala lateralia variabilia, sed nunquam magnopere longiora quam petala, fuscoviridia, saepe transversa. Petala erecta; lamina dense signata, c. 1 cm. longa, in ungue aequilongo. Labellum conspicue cuneatum, trilobatum, c. 1 cm. longum. Lobi laterales c. 8 mm. longi, oblique lanceolati, signati; lobus intermedius fuscopurpureus. Disci bracteae callosae fuscae, a carina fulva disjunctae. Columnae alae paululum altiores quam anthera acuta.

A fairly robust plant up to 60 cm. high. Leaves 2, linear, 25-35 cm. long. Floral bracts very abruptly acute. Flowers several on very erect slender pedicels, chrome yellow with deep purplish-brown markings or suffusions, rather large. Dorsal sepal erect, almost rhomboid, near the base heavily blotched, towards the anterior margins speckled. Lateral sepals variable, but never much longer than the petals, brown and green, often crossed. Petals erect; lamina densely spotted or blotched, about 1 cm. long, on a claw of equal length. Labellum conspicuously cuneate, trilobate, about 1 cm. long. Lateral lobes about 8 mm. long, obliquely lanceolate, blotched; mid-lobe almost wholly purplish-brown. Callous plates of the disc dark, separated by a chrome yellow keel. Wings of the column a little higher than the acute anther.

Kerr's Creek, between Dripstone and Orange, 10.1947; G. W. and P. Althofer.



Text-fig. 2.—Dissections of twelve *Diuris* flowers from the Central Western Slopes of New South Wales.

d.s., dorsal sepal; *l.s.*, lateral sepal; *p.* petal; *lab.*, labellum; *c.*, column.

1. *D. Althoferi*, n. sp.
2. *D. cucullata*, n. sp. A, side view of flower to show the horizontal dorsal sepal.
3. *D. cuneilabris*, n. sp.
4. *D. palachila* Rogers.
5. *D. flavopurpurea* Messm.
6. *D. platichila* R. D. Fitzg.
7. An undetermined form, allied to *D. semilunulata* Messm. Cumnock.
8. Another undetermined form. Dubbo.
9. *D. aurea* Sm.
10. *D. brevissima* R. D. Fitzg. and Nicholls.
11. Undetermined form from Kerr's Creek.
12. *D. lineata* Messm.

This species again is of very distinctive appearance. It is perhaps more nearly related to *D. flavopurpurea* Messmer than to any other species, but I do not see how they could be united without a very radical revision of descriptions; and difficulties of identification will be best avoided by keeping them separate.

There is another form from Kerr's Creek which I am quite unable to place in any known species; but it will probably be wise to wait for additional material before attempting to deal with it. Yet another form collected by the Althofer brothers, in the Cumnock area, appears to be closely related to *D. semitunulata* Messmer, from Queanbeyan. But in the Cumnock flower the lateral lobes of the labellum, although crescentic and quite as long as the mid-lobe, are only half as broad, i.e., half the width given for those of *D. semitunulata*.

The following is a description of a new variety of *Caladenia caerulea* R. Br.

Var. *heliotropica*, var. nov.

Flos purpurascens, major quam forma typica. Calli pallidi, in lobum intermedium albi. Lobus intermedius albus. Columna anguste alata.

Flower heliotrope, larger than in the typical form. Calli of the disc cream-coloured on white stalks, those on the mid-lobe pure white. Mid-lobe pure white. Column narrowly winged for nearly its whole length.

Ganoo Forest, Dubbo, 9.1947; G. W. and P. Althofer.

On receipt of the first specimen of this plant I was disposed to regard it as an undescribed species. Generally speaking, *C. caerulea* is one of the least variable species in the genus, being very constant both in form and colour, the latter almost sky-blue. Here was a plant from the Western Slopes, obviously related to *C. caerulea*, but with a bright heliotrope flower, and with differences of some importance in the floral details. At my request the collectors sent additional material. One of the new specimens was a typical *C. caerulea*, and two others were nearly so. In all cases the leaf was characteristic of Brown's species, broad-linear and almost decumbent. I concluded, therefore, that we must be content to give this attractive little Dubbo orchid varietal rank.

Supplementary Note.—Since the completion of this paper Mr. G. W. Althofer has sent in specimens of a diminutive *Prasophyllum* (section *Genoplesium*) found near Dripstone in March, 1948. Although the flowers are darker than those of Victorian and South Australian specimens seen by me, they appear to belong to the species *P. fuscoviride* Reeder. This has not previously been recorded from New South Wales. In Victoria it is strictly an inland species, occurring in areas which correspond fairly well with our Central Western Slopes.

SOME OBSERVATIONS ON MYRMECIA TARSATA SMITH.

By JOHN McAREAVEY, S.J.

[Read 30th June, 1948.]

INTRODUCTION.

Observations on *Myrmecia regularis* Crawley convinced Dr. W. M. Wheeler that the females of *Myrmecia* found their colonies in a very different manner from that used by the higher ants:

"I believe, therefore, that the *regularis* female makes her cells soon after her nuptial flight, and then leads the life of a recluse till October or November, occasionally breaking through the outer wall and foraging for food. With the return of spring in October, the more abundant food supply enables her to lay a number of eggs and to rear a few larvae with insect food which she captures on similar excursions. ("Colony Foundation Among Ants", p. 29, 1933.)

J. Clark, in "Notes on Australian Ants" (*Mem. Nat. Mus. Vict.*, 8, p. 7, 1934), queries Wheeler's statement that the female "leads the life of a recluse till October or November", and states that the female *M. forficata* rears her brood as early as April, and "all during the winter months she may be found foraging for food both for herself and larvae". It is probable that there is no contradiction here, for it appears that there is considerable variation in the times when the female oviposits. This variation would reconcile the fact that eggs have been found in a nest of *M. forficata* in April, and the fact that at the beginning of November an incipient colony of *M. nigriceps* contained young workers as well as cocoons and larvae, and with Wheeler's statement that *M. regularis* females lay a number of eggs in October. Observations of females in artificial nests show that some species begin to oviposit within a week of the nuptial flight, while others do not begin to lay until some months have passed. It has also been noted at Pymble that old nests of *M. eudoxia* contain almost fully developed larvae before even eggs appear in the nests of *M. tarsata*. Wheeler's statement seems correct, and the notes contained in this paper are a confirmation of many of the observations made by both Wheeler and Clark, while some additional information has been learned from *Myrmecia tarsata*. The vivid blue-green metallic colour, and the contrasting yellow mandibles and orange tip of the gaster give *M. tarsata* a very striking appearance, while the great number of its colonies in the sandstone country around Sydney provides opportunity for easy observation. Such were the reasons why this species was selected, but, as the notes will show, *M. tarsata* is well worth careful examination.

THE NUPTIAL FLIGHT.

Between the last two weeks of February and the beginning of April it is a common sight each year to find queens of *Myrmecia tarsata* wandering on the garden paths or even running along the floor inside Canisius College, Pymble. For some time it was presumed that the ordinary nuptial flight had taken place, and these were dealated queens seeking suitable places to dig nests and produce their colonies. The first doubt about the existence of true nuptial flights came in 1939, when examination of a number of nests of *M. tarsata* revealed only queens with completely undeveloped wings, which would be quite unsuitable for flight. These were thought to be merely freaks of nature, and since other species of *Myrmecia* collected in Victoria and New South Wales had queens with well-developed wings and a true nuptial flight, it was expected that some nest would contain *M. tarsata* queens with fully developed wings, if a more careful search were made.

Some years' absence from New South Wales caused the matter to be almost forgotten, but the problem arose again by mere chance. A number of males and workers had been captured to replace specimens in the collection. The afternoon was warm, and

it was a surprise to find that the males, excited by the heat, were attempting to mate with the workers. During the time they were observed only one male succeeded in mating, though for a considerable time as many as nine workers, each with a male firmly attached to the thorax, was repeatedly solicited. There could be no doubt about the actual mating of one of the pairs. At first the worker remained still for some seconds during which the male gradually relaxed his hold until he rested on his curved extended gaster with his body upright almost at right angles to the worker, and with his wings and legs limp in the air. Then the worker began to run quickly about the nest so that for four minutes the male, still in that strange position, was dragged around the glass nest. So still was he, that it was thought that he had been stung and was dead. As the worker suddenly began to climb the walls, the male fell backwards, and a struggle went on as the worker seized with mandibles any part of the male within reach. When the pair separated the worker chased the male, which promptly retreated out of reach.

This mating of male and worker brought back the problem of the nuptial flight of *M. tarsata*. If the male mated with workers on the ground it was possible that normally they mated on the ground with the queens, and this would remove the problem of the undeveloped wings of *M. tarsata* queens. On the first of March, 1946, a nest of *M. tarsata* was opened, and a number of males and queens collected. Of the twelve queens removed, two had small undeveloped wings, the others were wingless, but not difficult to distinguish from the smaller workers. These queens, with a number of males, were placed in a glass container. When this container was placed in the sun mating took exactly the same form as had been observed in the case of the worker and the male. It seems safe to conclude, therefore, that this is a normal method of mating, but two problems remain. Firstly, is there also a proper nuptial flight between fully winged specimens of the sexes, for the queens are often found in the upper rooms of the colony? This question can only be solved by finding a queen with fully developed wings, but up till this time none has been seen. Secondly, there is the question of the time when the young queens leave the parent nest. Do these queens, which are so common on the paths in March, leave the parent nest after mating, or do they leave the nest to meet the winged males which fly from nearby nests? The second view seems more likely, but observation is needed to confirm it. The nuptials of *M. tarsata* should be of considerable interest to biologists, for if there is no true nuptial flight, such as has been described in the case of other species of *Myrmecia*, we have a transitional stage in the evolution of the genus. The undeveloped wings of some of the queens of *M. tarsata* seem to point to a transition from the habit of mating in the air to that of mating on the ground, or *vice versa*. The large red bulldog ant, *M. eudoxia*, whose habits are nocturnal, has well-developed wings in both sexes. However, though the males and females do fly, it appears that the queens are not fertilized in flight, but while resting on some support such as a branch of a tree. This statement rests merely on personal observation and experiments in a large heated room. Froggatt's description of the nuptial flight of *M. gulosa* quoted by Wheeler in "Colony Foundation" appears to support this view that mating does not take place in the air.

"They (males and females of *M. gulosa*) were out in thousands, resting on the rocks and grass. The air was full of them, but they were chiefly flying in great numbers about the bushes where the males were copulating with the females. As soon as a male (and there were apparently hundreds of males to every female) captured a female on a bush, other males surrounded the couple till there was a struggling mass of ants forming a ball as big as one's fist. Then something seemed to give way, the ball would fall to the ground and the ants would scatter. As many as half a dozen of these balls would keep forming on every little bush and this went on throughout the morning."

This agrees with what has been observed here in all but the large numbers mentioned. After such mating, the queens remove their wings and set about digging a nest. Even the *M. tarsata* with the undeveloped wings remove their wings immediately after mating. The absence of winged or dealated females among specimens of *Promyrmecia aberrans* was noted by Wheeler (Colony Founding, p. 54) and the species *M. nigrocincta* appears to have females with undeveloped wings, so there is considerable need of further observation at this point. The period before laying eggs seems to vary

greatly even within the same species, and, as mentioned above, eggs may be laid within a week of mating, while in other cases months pass before the first eggs appear.

AN INCIPIENT COLONY.

On the 9th August, 1946, near a nest of *Leptomyrmex* sp., a queen of *M. tarsata* was found alone and in a crevice about one foot underground. The following day another *M. tarsata* queen was captured, but this one was climbing a tree stump some distance from the *Leptomyrmex* nest, and later the same day a third was noticed wandering on a garden path about three hundred yards from the stump. These three may have come from the same original parent nest. Certainly when placed together in an artificial nest all three were friendly. They dug a small nest of one passage, about two and a half inches long, but did not close the entrance to it as do most of the higher ants. During the next two months the queens spent most of the time outside their nest wandering in the sunlight which fell across part of the glass case. During that time they were fed on sugar-water and they refused all insect food. The ants were very lively and had a peculiar way of acting, that was so persistent that it drew the attention of the observer. Interpreted from a human point of view the actions seemed almost amorous. A queen would chase one of the other two for hours, and from time to time the two would stop, face each other, while one would rub her mouth-parts over the head and thorax of the other. During such meetings each ant would vibrate her antennae feverishly as ants do when they are excited. This peculiar action was certainly neither the mutual feeding or cleaning which often takes place in the nest.

Towards the end of September the small nest was opened, but there was no sign of eggs though the queens appeared to have settled down and spent more time in the common nest. However, about the middle of October, when the nest was examined again, a number of eggs were scattered about on the floor of the cell. It appears that the eggs of *Myrmecia* do not stick together in clusters as do the eggs of so many other ants. Wheeler noted this fact, and suggested that very probably the "salivary glands were too poorly developed to furnish the glutinous coating that keeps the eggs of higher ants together" (Colony Founding, p. 107). It is a common and rather absurd sight to see the large alert *Myrmecia* with their powerful mandibles carrying one single egg at a time from one part of the nest to another. Clark says in his account of *M. nigriscapa*, "the eggs hatch in from six to nine days, but six to seven months elapse before the first ants appear". The first part of the statement was not checked in these observations, but, as will appear further down, a *M. tarsata* worker took about four months to develop from the egg to adult stage. This, of course, was in artificial surroundings. The queens were fed on sugar-water until 10th November, when seven larvae which had hatched from the eggs were becoming restless in the nest. Then the diet was changed and the queens were supplied with beetles and other insects. These were readily taken, cut up, and given to the larvae, which devoured as much food as could be given to them. From 20th November until 14th December the ants were not fed, but the feeding on insect food continued after that date, and from time to time the nest was dampened carefully.

On 20th December one of the larvae was carefully banked up with moist earth by one of the queens, and the first cocoon was spun. A second cocoon was made on the 22nd, and on the following day four more were completed. The one remaining larva was small, and was rejected by the queens, while the other six in their cocoons were taken from the nest and placed in a dark corner of the glass case. One other important change took place: the queens from that time refused all insect food, and fed merely on nectar. It would seem that they are interested in insect food only when there are larvae present in the nest. On the 25th all the cocoons were taken back into the original cell.

We might say that up till this there had been only progress, and the small colony seemed successful. However, on the 26th December one of the queens died. Some disease may have killed her, but not long after the second queen was definitely killed by the third in the following way: On the 2nd January one of the queens was removed for the day,

and after she was returned to the nest she was attacked, killed and cut in two by the other queen. At the time it was difficult to explain this action, because up till the time the second queen was removed there had not been the least sign of hostility, and for nearly six months the three queens had lived together peacefully. However, von Buttel-Reepen, Mrazek, Wheeler, Wasmann, Meyer and others have observed a similar elimination of rivals by one female, in other genera, and Clark speaks of fighting between *Myrmecia* queens after the larvae have developed, so it appears that true haplometrosis obtains in the genus *Myrmecia*.

On the 31st January it was found that one of the cocoons had been opened, but there was no trace of the contents. A second cocoon was opened by the queen on the 4th February, and an almost perfectly developed worker was drawn out and partly eaten by the queen. During February all the cocoons were opened at intervals, since there was no interference with the queen in any way. A similar destruction of cocoons has been described by Dr. Haskins in the *Journal of the New York Entomological Society* for June, 1941: "When nine cocoons had accumulated, the females (in this case Ponerine ants of the species *Bothroponera soror*) began systematically to destroy the older ones, cutting them open and extracting and dismembering the pupae, which were those of already partially pigmented young workers. Seven cocoons were so destroyed, when the remaining two were artificially isolated in an attempt to save them." It is interesting to note that the *M. tarsata* queen was well fed on nectar, and refused all insect food that was offered, so that hunger can hardly have been the cause of the destruction of the cocoons. The last cocoon was opened on 26th February, and immediately the naked pupa was taken from the nest. It was an almost completely pigmented worker, which could move its antennae and legs slightly, but was not strong enough to stretch out fully and stand up. The queen, now alone, remained in her cell, and though she came out for food when the case was darkened, she avoided the light as much as possible, as do mature queens of the higher ants. This queen was still alive in June, 1947, and after having adopted a great number of cocoons supplied to her from other nests, had a number of these alien workers to care for her, though she laid no more eggs.

PUPAE AND CALLOWS.

We might say that the young of *M. tarsata* are left much to themselves, for even during the larval stage they do not receive the attention which the higher ants lavish on their brood. They are not fed by regurgitation, but insect food cut up by the hunters is merely left close to them. This they eagerly devour, and occasionally, if supplies are low, the more vigorous larvae attack and eat their weaker sisters. Seeing the larvae are left to fend for themselves, the interesting question arises, can the young ants emerge from the cocoons unaided by adult workers? Other primitive ants such as the American *Stigmatomma pallipes* can do this, and numbers of workers of *Amblyopone australis* have been observed leaving their cocoons completely unaided. During February, when the pupae in their cocoons are almost fully developed, numbers of cocoons have been isolated each year, but so far we have not observed a single ant emerge. This year over a hundred cocoons were isolated, and for a week the insects wriggled and scratched within the cocoon, but could not break through. It is possible to be stung through the cocoon, and occasionally an ant has pierced the cocoon with the tips of the mandibles, but seemingly could get no further. Examining some of the cocoons after the insects had ceased to scratch on the inside, perfectly formed insects were found, quite free of all pupal wrappings, but dead. On the other hand, when lively pupae were placed with the *M. tarsata* queen, she has opened the cocoons immediately. The workers which emerged were deeply pigmented, and all males had their wings fully developed.

It has been suggested that during the very short period before the tegument hardens, the callows "learn" from mature ants. *M. tarsata* "learns" no more than does the solitary hunting wasp "learn" the art of paralysing its victims or of building its nest. From the beginning it is fully equipped for its life. Individuals of *M. tarsata*, which have never had contact with adult ants, act exactly as do the workers of a well-

established nest. Within an hour of being placed in the artificial nest such ants have begun to work excavating a nest, and when hunger urged them they have gone in search of nectar. They have taken care of all cocoons given to them, opening them to free the young ants. When cocoons of alien species were given to them they immediately rejected them. An equal number of partly opened cocoons of *M. tarsata* and *M. eudoxia* were placed in the same box and as the young emerged, and even while they still had pieces of the pupal membranes adhering to their legs and gaster, they began to fight to the death, until only one species remained.

When the workers emerge from the cocoons they are fully developed, and the first brood workers, raised in an artificial nest, are no smaller than those of later broods. This can be explained by the fact that even the first brood larvae are well fed on insect food by the queen, which hunts widely for food, while in the higher ants the queen, being completely a recluse after her nuptial flight, can provide only scanty food by regurgitation. This is a personal observation, and it is to be noted that Clark (1925, pp. 135-144) says: "the first brood are always small examples, owing no doubt to the scarcity of food, while the second brood and subsequent broods usually are of normal size, as the workers procure the food. Sometimes a few small workers may be found, particularly in spring. These are regarded by some naturalists as minor workers, but I consider that they are merely the result of a scarcity of food during the winter months." This raises the question of the polymorphism of these primitive ants. It is certainly true that there are very few species in which there is not very great diversity in size among the workers. In *M. tarsata*, *M. gulosa*, *M. eudoxia*, *M. nigriceps* and *M. forficata*, to mention only a few species personally examined carefully, all nests contain numbers of very small workers. These small workers are often much less than half the size of their larger sisters, and there are intermediate sizes. There is only difference in size, however, not the difference in head structure, which one finds in the true polymorphic genera such as *Pheidole*, and many of the genera of the sub-family Formicinae. Since I hesitate to describe *Myrmecia* as polymorphic and regard the difference in size as accidental though very common, I leave this final question for further investigation.

SUMMARY.

Since so little observation has been made on the numerous species of *Myrmecia*, it would be unwise to draw general conclusions from this particular study of *M. tarsata*. This species appears to have no true nuptial flight but mates on the ground, though at the same time the females possess small undeveloped wings which they discard after mating. The female forages for food during the winter months while she is rearing her brood. She is nectarivorous herself, but she feeds her brood entirely on insect food, which she cuts up and places near the larvae. Several females may build and live in the same nest chamber, but as the larvae develop one queen eliminates the others. The young ants need assistance when it is time to emerge from the cocoons. To what extent these habits are common to other *Myrmecia* can only be discovered by further observations.

References.

- CLARK, J., 1925.—*Vict. Nat.*, 42: 135-144.
 ———, 1934.—Notes on Australian Ants. *Mem. Nat. Mus. Vict.*, 8: 5-7.
 WHEELER, W. M., 1932.—How the Primitive Ants of Australia Start their Colonies. *Science*, N.S., 76: 532.
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 HASKINS, C. P., 1941.—Notes on the Method of Colony Foundation of Ponerine Ants. *Journ. N. York ent. Soc.*, 49: 211-216.

In later years several new genera such as *Paquerina* H. Cass (1825), *Brachystephium* Less. (1832), *Steiroglossa* DC. (1838), *Silphiosperma* Steetz (1844) and *Ctenosperma* F. Muell. ex Pfeiff. (1874) were described, based on isolated specimens. As collecting in Australia became more extensive, the apparent discontinuities between these separate genera were diminished, their characters were recognized as of specific status rather than of generic significance, and the original generic concept of *Brachycome* was expanded to cover them.

Distribution of the Genus.

Although species of *Brachycome* are recorded from Assam (*B. Assamica* C. B. Clarke), Tropical Africa (*B. Mossambicensis* Oliver and Hiern., and *B. palustris* O. Hoffm.) and Bolivia (*B. hispida* Klatt.), the author is of the opinion that more critical examination of these specimens will show them to be generically distinct, though no doubt closely allied. Efforts to trace specimens of the above species have been unsuccessful, so that on the evidence available, *Brachycome* is considered to be confined to Australia and New Zealand, with a single unconfirmed record from Papua.

From the specimens examined, this genus appears to be most widely distributed throughout the Eastern States and South Australia. Perhaps it is more than a coincidence that it is in these portions of Australia that collectors have been most active. Only one species (*B. Clementii* Domin.) is recorded from the Kimberley district of Western Australia, and unfortunately the author has been unable to trace any specimens of this species. For this reason, *B. Clementii* has not been included in the key to the species, and the original description has been merely translated. Only more intensive collecting in Western Australia and the Northern Territory particularly will decide whether the present known distribution is correct.

Distribution of the Subgenera.

From Table 1 it is apparent that in the number of component species the subgenus *Eubrachycome** predominates over the subgenus *Metabrachycome** in Eastern Australia, reaching its relative maximum in New South Wales, thereafter steadily declining in its percentage of species from east to west. In Western Australia only one species belongs to the subgenus *Eubrachycome*.

The fact that comparatively few species are found in Tasmania indicates that speciation has been most active on the mainland of Australia but migration southward was prevented by Bass Strait.

TABLE 1.

Distribution of Species in the Subgenera Eubrachycome and Metabrachycome.

	Total number of Species.	Species of Subgenus <i>Eubrachy-</i> <i>come.</i>	Species of Subgenus <i>Metabrachy-</i> <i>come.</i>	<i>Eubrachy-</i> <i>come.</i> %	<i>Metabrachy-</i> <i>come.</i> %
Queensland	20	16	4	80	20
New South Wales	33	28	5	84.5	15.5
Victoria	26	20	6	76.9	23.1
Tasmania	9	7	2	77.7	22.3
South Australia	24	17	7	70.8	29.2
Western Australia	14	1	13	7.1	92.9

Nomenclature.

Considerable changes in nomenclature of the species have been made necessary by strict adherence to the International Rules of Botanical Nomenclature. Many of these changes are regrettable in that they concern well-known species and involve abandoning some names in wide use in favour of earlier synonyms. Such a state of affairs is inevitable in the revision of any genus, and is unavoidable if stability of nomenclature is to be achieved.

* Defined under Taxonomy, p. 148.

Syntype material of nearly all described species and varieties, whether valid or otherwise, has been traced, and type selection made, the selected specimens serving as a basis of comparison for all specimens listed. The actual method of type selection, where not obvious, has been discussed in connection with the species concerned. No nomination of lectotype or lectoparatype has been made in the absence of considerable evidence that the particular specimens formed part of an authentic syntype series. Where any doubt exists that the original author actually handled a certain specimen, even though it is labelled with the same data as is quoted in his description, Furtado's term "haptotype" is employed.

A large number of specimens belonging to the National Herbarium, Melbourne, was used by Bentham in the preparation of his *Flora Australiensis*, and subsequently returned by him to that institution. The labels accompanying these specimens are all marked ("B"), and when one of these was quoted by Bentham in a description of a new species or variety, that specimen has been considered to be an authentic syntype of equal value with a duplicate which may have been retained by him.

As far as possible lectoparatypes were selected which were toptotypical with and of the same date of collecting as the lectotype. In a syntype series, the most complete specimen was nominated lectotype, and the remainder lectoparatypes.

The terminology used throughout is that of Davis and Lee (1944), with one additional term, haptotype, which has been applied to a specimen bearing the type data, but about which there exists some doubt that it was actually handled by the original author.

Categories.

The term subgenus has been employed for each of the two major groups of this genus, and indicates the author's opinion that the two subgenera are incipient genera. No attempt has been made to define the term species, it being considered that specific concepts vary with the genera concerned. The species undoubtedly represents a real entity of nature, but its limits can be recognized only after experience has been gained by the handling of large numbers of specimens. During recent years attempts have been made by various authors to arrive at a universal species definition, but in the opinion of the present author, none of them would enable the recognition of a species as such. This fact was recognized by Darwin (1859), whose remarks were condensed by Mayr (1942) into possibly the truest, though still by no means satisfactory, definition, that "a species is a systematic unit which is considered a species by a competent systematist (preferably a specialist of the group)".

Except in exceptional circumstances, it has not been considered advisable to describe any new taxonomic group from a single specimen. Consequently, in the following pages, certain exceptional specimens have been noted and commented on from time to time. These specimens may be found to represent new species or varieties if further similar materials should come to hand, but in the meantime it is better to consider them aberrant individuals of an existing species rather than to erect new names which may become further additions to a long synonymy.

As a working hypothesis, variation in the fruits has been considered a specific character, and has been found to be discontinuous, the discontinuities representing gaps between species. Constant vegetative variation, on the other hand, has been given varietal status, the fruits of all varieties of any one species being identical. When one or more varieties are described in a species, the specific name is repeated in varietal status for the population to which the epithet was originally applied. This corresponds to the var. *typica* of various authors.

Incipient species would be expected to show small but constant variation from the parent species in characters of the fruit and not necessarily in vegetative characters. Such variation, however, has not been found as a constant feature of any population, so that the term subspecies has not been employed.

As has been found in all critical revisions, the discontinuities between species are not of uniform size and recognizable species groups tend to be formed in which certain

orthogenic trends can be traced. These groups or clusters of species are the *Artenkreis* of Rensch and the *Superspecies* of Mayr, defined by the latter author (1942, p. 169): "A superspecies consists of a monophyletic group of geographically representative (allopatric) species which are morphologically too distinct to be included in one species." Each such group has been given the epithet of the most primitive component species, with superspecific status.

In order to be consistent throughout it has been necessary to formulate and to adhere strictly to certain rules. This, in a few cases, has led to apparent inconsistencies which require explanation. Separate status has not been allowed on the degree of development of a particular character, but only on the possession of a new character not shown by other members of a particular population. In any reasonably large series a certain amount of variation is to be expected in all characters, and where this is extreme, the question arises as to whether this population should be treated as a single unit or subdivided. Throughout this revision taxonomic treatment has depended on the answer to the question, "Is this particular variation in this particular population continuous or discontinuous?" If the former applies, then the population is treated as a single unit irrespective of the extremes reached in variation of the character under consideration. If the variation is discontinuous, then separate status is recognized. Application of this principle has led to all woolly-hairy specimens of *B. ciliaris* being included in var. *lanuginosa*, even though only a few woolly hairs may be present in the leaf axils. In *B. marginata* even densely woolly specimens are included under var. *marginata* with those in which the sparse woolly hairs can be found only with the aid of a strong lens. This treatment is admittedly arbitrary but does at least introduce some measure of consistency, and in a large and continuously variable species no useful purpose is served by anticipating evolution in an attempt to construct watertight groups where none, in fact, exist.

Evaluation of Taxonomic Characters.

Under appropriate headings the various portions of the plant have been discussed from the point of view of their taxonomic value. It should, however, be pointed out that whereas many characters in themselves are too variable to be of primary taxonomic importance, certain combinations tend to occur in certain species. The recognition of these frequently indefinable combinations becomes possible only with the handling of large numbers of specimens, and enables the accurate determination of those lacking primary diagnostic characters.

Habit.—Environmental factors exert a considerable influence on habit, consequently a wide variation has been encountered, though the vast bulk of individuals of each species conforms to a general plan which is referred to as being "typical" of the species.

Leaves.—Within relatively wide limits the leaves conform to the same type within a species or variety, but considerable variation is common between upper and lower leaves. It is in this character that convergence is most marked, and certain species (e.g. *B. debilis* and *B. leptocarpa*) are vegetatively identical. Usually in any species continuous leaf variation occurs, but some species fall into discontinuous groups on leaf characters, these groups then being nominated varieties.

Indumentum.—Although some species are glabrous, an indumentum of some kind is frequently present on the stem, and sometimes the leaves. The degree of development of the indumentum does not appear to be correlated with altitude or climate, though further work may show it to be related to other ecological factors. Unfortunately relevant ecological data is rarely recorded by collectors. The taxonomic importance of the indumentum varies in different species, so that in some it has proved to be a varietal criterion, whereas in others it is a character of no taxonomic value, according to whether glabrous plants are also known or not. The degree of development of the indumentum cannot be considered of taxonomic importance, only its presence or absence.

Capitula.—These are very uniform throughout the genus, and are borne either on a scape or on a peduncle arising from a more or less branching stem. Considerable specific variation in size is encountered, but intraspecific variation is slight and largely confined

to the number of rays present. Unless otherwise stated, in this paper the diameter of the capitula excludes the ray florets.

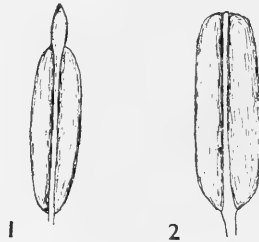
Involucral bracts occur usually in two whorls, but in *B. cardiocarpa* and *B. latisquamea*, three or even four whorls may be present. The term "whorl" is loosely applied, since the bracts occur in a compressed spiral. The shape of the bracts is very variable, even within a species, the inner ones being commonly narrower and more acute than the outer. In the specific descriptions, the measurements are those of the outer bracts.

Ray florets are consistently strap-shaped, the breadth being seldom correlated with the number present. Though measurements have been included in all descriptions, they are largely for the sake of completeness and are of no taxonomic significance. The usual colours are blue, mauve or white, with sometimes a pinkish tinge. Only one population (*B. marginata* var. *chrysoglossa*) is recorded in which the rays are yellow at maturity. A change of colour has been noted on several occasions when white rays changed to blue or mauve a few hours after being picked. The ray florets of *B. marginata* are frequently yellow when first expanded, changing later to white, a phenomenon which has led to the diagnosis of many specimens of this species as *B. chrysoglossa*. In all living specimens observed by the author, the rays became closely rolled downwards at sundown, expanding again a few hours after dawn.

Disc florets are constant throughout the genus, and are consistently pale to deep yellow.

Stigmas have not been found to be of any specific importance, being invariably lanceolate with glandular papillae on the outside.

Anthers are proximally obtuse, and distally the connective is either truncate or produced beyond the pollen sacs into a relatively long terminal appendage. This latter character has been found to be of considerable taxonomic importance, and on it a marked dichotomy is apparent in the genus. The presence or absence of the distal anther appendage is discernible in the earliest bud stage, and consequently this character is of importance in distinguishing between two species which are vegetatively very similar (i.e., *B. exilis* and *B. leptocarpa*).



Text-figures 1-2. Anthers. $\times 25$.

1. Anther, subgenus *Eubrachycome*.
2. Anther, subgenus *Metabrachycome*.

Receptacle.—The general shape of the receptacle can be regarded as a supporting taxonomic character, but it is of little significance alone, and the proportion of breadth to height is variable. The degree of pitting is sometimes of importance.

Fruits.—The characters of the mature fruits are of primary taxonomic importance, and it is on these that the whole classification is based. As already indicated, there are instances of extreme vegetative convergence in which diagnosis cannot be made in the absence of fruits. Indication of the development of a wing can usually be seen at an early stage, but the degree of turgidity, colour, presence of tubercles and longitudinal folds, which are characteristic of certain species, are not indicated until maturity. It has been noted that fruits occupying an apical position on the receptacle are usually abortive. This is probably due to the earlier maturing of peripheral

flowers, so that the central ones are either not fertilized or are prevented from maturing by the earlier development of the peripheral fruit which commandeers the bulk of the vascular supply. Distortion of fruits by lateral pressure is noticeable in densely packed heads, such as those of *B. goniocarpa* and *B. diversifolia*, in which the typical quadrangular shape gives place at the periphery to triangular fruits which may be strongly curved inwards. The flat winged fruits of *B. marginata*, *B. cardiocarpa* and *B. nivalis* are less densely packed, and lateral pressure is slight, so that the characteristic shape is largely retained throughout the head. The phenomenon of dimorphic fruits is seen only in *B. ciliaris*.

Specimens Examined.

Over 1,800 specimens have been critically examined and are listed under the appropriate species. These specimens were loaned for the purpose by the Directors of the various State Herbaria and private collectors, the source in each case being indicated as follows:

National Herbarium, Melbourne (MEL).
 National Herbarium, Sydney (NSW).
 Brisbane Herbarium (BRI).
 Adelaide University (AD).
 Perth Herbarium (PERTH).
 Hobart Museum (HO).
 J. M. Black (JMB).
 J. B. Cleland (JBC).
 R. A. Black (RAB).
 Research Station, Cunnamulla (CSIR).
 Gray Herbarium, Harvard (HARVARD).
 De Candolle Herbarium, Geneva (GENEVA).
 Natural History Museum, Paris (PARIS).

Many of the specimens, inevitably, were in flower only, and these have been marked with an asterisk, as, although the author is satisfied with their determination, the possibility of a mis-identification, in the absence of fruits, cannot be overlooked.

All specimens have been listed in the manner adopted by Bentham, in geographic sequence from north to south and east to west. In widely distributed species it has sometimes been necessary to divide a State into an eastern and western section, and list specimens in each in a north to south sequence. Distribution maps are supplied for all the species.

Specific Descriptions.

Each species has been redescribed from the specimens available, and in nearly every case the series was considerably longer than that on which the original description was based. As a result the specific concepts have been enlarged to cover forms and variations unknown to the original authors. Although various measurements are given, they should be taken as of little absolute significance and are included mainly for completeness.

Where one or more varieties exist, a general specific description has been given which embraces them all.

The description of each species and variety is accompanied by figures illustrating its habit and fruit. Where possible, the former is an accurate drawing of the lectotype, but when this specimen was found to be unsatisfactorily preserved the figure has been made from other and usually more recent material. Since variation between involucre bracts, even on the same capitulum, may be so wide, it was considered that no useful purpose would be served by figuring one or two.

All figures of fruits are camera lucida drawings, and those of complete specimens are based on outline tracings so that a high degree of accuracy has been attained.

TAXONOMY.

COMPOSITAE, tribe ASTEROIDEA.

Brachycome Cass., *Dict. Sci. Nat.*, 37, (1825), 491.

Synonymy: *Brachyscome* Cass., *Bull. Soc. Philom. Paris* (1817), 199. (Corrected to *Brachycome* by Cassini in 1825.)

Paquerina Cass., *Dict. Sci. Nat.*, xxxvii (1825), 492.

Brachystephium Less., *Syn. Comp.* (1832), 388.

Steiroglossa DC., *Prod.* vi (1838), 38.

Silphiosperma Steetz in *Lehm. Pl. Preiss.*, 1 (1844), 433.

Ctenosperma F. Muell. ex Pfeiff., 1 (1874), 936.

Annual or perennial herbs, rarely undershrubs, with entire or variously dissected radical and/or cauline leaves. *Inflorescence* a capitulum, solitary or numerous, heterogamous, each borne either on a scape or peduncle arising from a branching stem. *Involucral bracts* green, either glabrous or shortly glandular or woolly on the outer surface, with scarious, entire or torn margins, and arranged in a compressed spiral forming two, or occasionally three, rows of bracts. *Ray florets* female, ligulate, white, blue, mauve, pink or occasionally yellow, and occur in a single row round the periphery of the capitulum. *Disc florets* hermaphrodite, tubular, 5-toothed, yellow. *Anthers* obtuse at the base, and the connective either terminates distally on a level with the pollen sacs or is produced beyond them into a lanceolate appendage. *Branches of the style* are lanceolate, papillose on the outer side and enclosing the stigmatic lines. *Receptacle* slightly to very steeply convex, naked, pitted or unpitted. *Fruit* an inferior achene, flattened or turgid; body of fruit glabrous, glandular or tuberculate, sometimes with longitudinal folds or grooves. Pappus consists of free or occasionally united bristles, from microscopic to comparatively large, but sometimes absent.

Type species: *Brachycome aculeata* (Labill.) Less.

Key to the subgenera of Brachycome.

Anther connective produced beyond the pollen-sacs to form a lanceolate appendage (Fig. 1) 1. Subgenus *Eubrachycome*
 Anther connective without any such distal appendage (Fig. 2) 2. Subgenus *Metabrachycome*

1. Subgenus *Eubrachycome*.*Key to the Superspecies.*

- (1). Fruit wingless.
 (2). Fruit flattened, obovate-cuneate to narrow obovate.
 (3). Fruit glabrous or with a few straight hairs. Leaves entire, toothed or pinnatisect, radical and/or cauline 1. Superspecies *tenuiscapa*.
 (3)* Fruit bearing scattered short glandular hairs. Leaves toothed or pinnatisect 6. Superspecies *tesquorum*.
 (2)* Fruit thick or only slightly flattened.
 (4). Fruit obovate, tuberculate, usually with a smooth margin. Pappus white, minute to moderate in size. Leaves cauline 3. Superspecies *basaltica*.
 (4)* Fruit narrow to broad-cuneate, with smooth or tuberculate horseshoe-shaped lateral folds. Pappus conspicuous, obliquely placed (except in *B. Readeri*) and often stellate. Leaves cauline. 5. Superspecies *diversifolia*.
 (1)* Fruit winged (except in *B. leptocarpa* and *B. graminea*).
 (5). Body sharply demarcated from wing by a groove or fold. Wing thin and membranous, or inflated and spongy 2. Superspecies *leptocarpa*.
 (5)* Body not sharply demarcated from wing (except in *B. Muelleri* and *B. Muelleroides*). Wing always thin, either flat or curved inwards 4. Superspecies *aculeata*.

1. Superspecies *tenuiscapa*.*Key to the Species.*

- (1). Herbs with a glandular-septate indumentum. Leaves oblanceolate to ovate-cuneate, distally dentate, with sheathing bases. Fruit smooth, 1.2-1.8 mm. long, 0.9 mm. broad, with slightly thickened margins. Pappus short and white .. 1. *B. tenuiscapa*.
 (1)* Glabrous herbs.
 (2). Leaves entire, toothed or crenate.
 (3). Fruit 2.3-3 mm. long, 0.8-1.2 mm. broad, glabrous with slightly thickened smooth margins. Leaves linear to oblanceolate, acute, entire 2. *B. scapigera*.

- (3).* Fruit 3 mm. long, 1.4 mm. broad, with relatively long straight hairs on each flat surface, and a shallow longitudinal groove down the outer edge of each slightly thickened margin. Leaves oblong-cuneate to elliptical, entire, crenate to acutely toothed distally 3. *B. decipiens*.
- (2).* Leaves pinnatisect, the segments entire or lobed. Fruit 0.9-1.7 mm. long, 0.5-0.9 mm. broad, with two longitudinal folds on each face. Pappus short, bristles of unequal length 4. *B. Sturtii*.

2. Superspecies *leptocarpa*.*Key to the Species.*

- (1). Body of fruit not tuberculate.
- (2). Fruit obovate or linear-cuneate, the body more or less glandular hairy, with a thin wing (except in *B. leptocarpa*); annual herbs.
- (3). Fruit 1.5-2 mm. long, with long glandular hairs on the body, and a conspicuous pappus. Wings entire, shallowly dissected, or absent. Septate-hairy herbs with entire to pinnatisect leaves, usually only cauline.
- (4). Fruit 0.5 mm. broad, linear-cuneate with numerous apically rolled hairs. Wings absent 5. *B. leptocarpa*.
- (4).* Fruit 1 mm. broad, obovate; body oblong with few hairs. Wings entire or shallowly dissected 6. *B. debilis*.
- (3).* Fruit 0.9-1.1 mm. long, 0.6-0.8 mm. broad, the body with usually 2 longitudinal grooves and microscopic glandular hairs, and a short pappus. Glabrous herbs with a basal cluster of pinnatisect radical leaves ... 7. *B. ptychocarpa*.
- (2).* Fruit obovate to oblong-cuneate, with a glabrous body and smooth inflated wings. Perennial herbs with mostly cauline leaves.
- (5). Fruit 2 mm. long, 1.6 mm. broad, obovate, turgid and slightly flattened, the body completely enclosed by the inflated wings, so that the fruit appear to be wingless. Pappus very small 14. *B. graminea*.
- (5).* Fruit 2-4.2 mm. long, 0.8-2.5 mm. broad, the body sharply defined and the wings more or less glandular-hairy along the outer edge. Pappus conspicuous.
- (6). Glabrous herbs. Leaves cauline, entire or with 1-4 linear lobes. Fruit 2 mm. long, 0.8 mm. broad, oblong-cuneate and flattened, the body with 2 or 3 longitudinal folds, the wings almost as broad as the body, with short glandular hairs along the edge 12. *B. radicans*.
- (6).* Glabrous or more or less septate-hairy herbs. Leaves once or twice pinnatisect. Fruit with long glandular hairs along the outer edge of the wings, and a very large pappus.
- (7). Leaves radical and pinnatisect, forming a basal cluster. Fruit broad-cuneate, 3.2-4.2 mm. long, 1.6-2.5 mm. broad, the wings very turgid. Pappus bristles of unequal length, grouped in bundles 13. *B. uncariloba*.
- (7).* Leaves radical and cauline, sometimes twice pinnatisect. Fruit oblong-cuneate, 2-2.7 mm. long, 1.2 mm. broad, strongly curved, the wings distally expanded. Pappus bristles conspicuous, not grouped in bundles .. 15. *B. campylocarpa*.
- (1).* Body of fruit tuberculate.
- (8). Fruit narrow-cuneate, 2-2.2 mm. long, 0.9 mm. broad, with large laterally flattened tubercles, and narrow wings. Pappus bristles long and of irregular length. Glabrous or sparsely glandular-pubescent herbs with cauline, entire or irregularly pinnatifid leaves 8. *B. angustifolia*.
- (8).* Fruit obovate to oblong-cuneate with broad entire or dissected wings.
- (9). Glabrous herbs. Tubercles on fruit small.
- (10). Leaves radical, entire, toothed or pinnatisect. Fruit 1.5 mm. long, 1 mm. broad, broadly obovate-cuneate, the tubercles confined to the central region of the body. The wings entire, about half the breadth of the body 9. *B. dissectifolia*.
- (10).* Leaves cauline, pinnatifid to pinnatipartite. Fruit 2.5 mm. long, 1.8 mm. broad, the tubercles small and scattered, the wings as broad as, or exceeding the breadth of the body, shallowly and irregularly incised .. 10. *B. procumbens*.
- (9).* Glandular-pubescent to septate hairy herbs with radical and cauline leaves, either pinnatifid or distally toothed. Fruit 1.5 mm. long, 1-1.2 mm. broad, obovate, the wings entire with relatively long glandular hairs along the edge. Tubercles on body confluent, giving a bladder-like appearance to each face 11. *B. Whitei*.

3. Superspecies *basaltica*.*Key to the Species.*

- (1). Erect glabrous herbs with radical and/or cauline, linear or broad-lanceolate leaves. Fruit narrow-cuneate to obovate, somewhat flattened, with smooth margins. Pappus a minute irregularly broken rim 16. *B. basaltica*.

- (1).* Ascending or weakly erect herbs with toothed or divided cauline leaves. Radical leaves present only on young plants. Fruit usually turgid. Pappus of capillary bristles.
- (2). Pappus conspicuous. Leaves pinnatifid to pinnatisect or pinnatipartite.
- (3). Pappus bristles all free. Herbs with glandular and septate-hairy indumentum.
- (4). Fruit oblong, much flattened, brown, with small tubercles. Margin expanded, wing-like and irregularly incised. Pappus conspicuous 17. *B. ascendens*.
- (4).* Fruit obovate to subcylindrical, usually slightly flattened with a smooth margin, dark brown to black. Pappus short to conspicuous.
- (5). Fruit obovate-cuneate, 1-1.8 mm. long, 0.7-0.9 mm. broad, the margins always smooth, the pappus short. Radical leaves seldom present; cauline leaves pinnatifid to pinnatisect or almost crenate, always a few on each plant opposite. Ascending or weakly erect herbs with a more or less glandular-pubescent indumentum 18. *B. microcarpa*.
- (5).* Fruit obovate to subcylindrical, 2-2.5 mm. long, 1 mm. broad, with large tubercles either extending round the entire fruit or leaving a smooth margin. Pappus usually conspicuous. Radical leaves often present; cauline leaves always alternate, pinnatifid to pinnatipartite. Erect herbs with a glandular and septate-hairy indumentum 20. *B. melanocarpa*.
- (3).* Pappus bristles spreading, of unequal length and grouped in bundles. Fruit slightly flattened, obovate-cuneate with small tubercles and smooth margins. Glabrous herbs. Leaves once or twice pinnatisect to pinnatipartite 21. *B. multifida*.
- (2).* Pappus microscopic. Glandular and septate-hairy herbs. Leaves cauline and acutely toothed distally 19. *B. Nova-Anglica*.

4. Superspecies *aculeata*.

Key to the Species.

- (1). Fruit flat, with a broad, entire or dissected wing.
- (2). Majority of leaves cauline. Peduncles axillary or terminal, sometimes scape-like.
- (3). Body of fruit with short scattered glandular hairs, the wing partially dissected. 22. *B. aculeata*.
- (3).* Body of fruit with short glandular hairs or finger-like tubercles, the wing entire or completely dissected.
- (4). Tubercles on fruit, when present, cylindrical, the wing completely and irregularly dissected 23. *B. marginata*.
- (4).* Tubercles laterally flattened, the wing entire or undulating dissected 24. *B. papillosa*.
- (2).* Leaves radical. Scapes robust.
- (5). Leaves entire, linear and grasslike. Body of fruit glabrous 28. *B. cardiocarpa*.
- (5).* Leaves entire or irregularly pinnatipartite to twice pinnatisect. Body of fruit with short glandular hairs 29. *B. nivalis*.
- (1).* Fruit markedly curved, the body glabrous or with short scattered glandular hairs, the wings entire or slightly incised. Leaves cauline and sessile.
- (6). Glandular and more or less woolly-hairy herbs with pinnatipartite leaves. Wings flat and slightly dissected 25. *B. curvicarpa*.
- (6).* Glabrous herbs with stem-clasping leaves. One aspect of the body of the fruit almost obscured by the infolded wings.
- (7). Leaves irregularly pinnatipartite. Fruit about 2 mm. long, 1.5 mm. broad with a striate terete body. Pappus microscopic 26. *B. Muellerei*.
- (7).* Leaves narrow-linear to linear, entire or with a few proximal filiform lobes. Fruit 0.9 mm. long, 0.6 mm. broad, the body linear, not striate. Pappus about one-fifth the length of the fruit 27. *B. Muelleroides*.

5. Superspecies *diversifolia*.

Key to the Species.

- (1). Leaves pinnatisect to pinnatipartite. Longitudinal folds entire or tuberculate. Pappus obliquely placed and conspicuous, simple or stellate.
- (2). Fruit narrow-cuneate to cuneate, 2-2.8 mm. long, 0.9-1 mm. broad.
- (3). Herbs with glandular and septate-hairy indumentum. Leaves frequently twice pinnatisect. Fruit narrow-cuneate, 2-2.8 mm. long, 0.9 mm. broad 30. *B. diversifolia*.
- (3).* Glabrous herbs with pinnatisect leaves. Fruit cuneate, 2 mm. long, 1 mm. broad 31. *B. segmentosa*.
- (2).* Fruit broad-cuneate, 1.2-2.4 mm. long, 0.5-2 mm. broad.
- (4). Herbs with glandular and septate-hairy indumentum. Fruit glabrous, with longitudinal folds broken up into large tubercles. Pappus stellate 32. *B. gonicarpa*.
- (4).* Glabrous herbs. Longitudinal folds on fruit entire, with long glandular hairs between them. Pappus of simple bristles 34. *B. eriogona*.
- (1).* Leaves pinnatisect. Longitudinal folds bear inflexed finger-like projections. Pappus large, centrally placed and stellate 33. *B. Readeri*.

6. Superspecies *tesquorum*.

Key to the Species.

- (1). Leaves oblanceolate, entire or with a few narrow teeth. Fruit narrow-obovate, flattened, glandular, with two inconspicuous longitudinal folds on each face. Pappus absent 35. *B. tesquorum*.
- (1)* Leaves bipinnatifid. Fruit narrow-cuneate, flattened, smooth, with a few scattered glandular hairs. Pappus minute 36. *B. Blackii*.

Subgenus *Metabrachycome*.

Key to the Superspecies.

- (1). Fruit dimorphic 8. Superspecies *trachycarpa*.
- (1)* Fruit not dimorphic.
 - (2). Fruit bear membranous wings.
 - (3). Annual or perennial herbs not exceeding 30 cm. in height, with pinnatisect leaves. Fruit not exceeding 3 mm. in length; pappus of capillary bristles.
 - (4). Glandular-hairy perennials with crowded cauline leaves. Fruit flat, obovate, 2.2-2.9 mm. long, 1.1-1.5 mm. broad, with narrow, entire or irregularly and shallowly dissected wings 8. Superspecies *trachycarpa*.
 - (4)* Septate-hairy annuals with mainly radical leaves. Fruit cuneate, 2.6 mm. long, 1.5 mm. broad; body flattened proximally, and distally dilated; wings narrow, fringed with long glandular hairs 9. Superspecies *ciliocarpa*.
 - (3)* Woody perennials up to 2 metres in height, with entire cauline leaves. Fruit broadly obovate, exceeding 3 mm. in length; pappus a ring of short irregular teeth 10. Superspecies *latisquamea*.
 - (2)* Fruit not winged.
 - (5). Pappus very conspicuous. Fruit cuneate to oblong-cuneate, flattened or shouldered, and bearing long glandular hairs 9. Superspecies *ciliocarpa*.
 - (5)* Pappus minute or absent. Fruit more or less flattened, seldom thick.
 - (6). Annual herbs with entire or pinnatisect cauline leaves. Ray florets very short. Fruit flat, margin wing-like and deeply dissected into claw-like segments or narrow and entire; pappus absent 11. Superspecies *Silphiosperma*.
 - (6)* Annuals or perennials with radical and/or cauline leaves. Ray florets conspicuous. Fruit obovate-cuneate to clavate. Leaves entire or pinnatisect.
 - (7). Fruit smooth, sometimes thick or shouldered; pappus sometimes absent 7. Superspecies *iberidifolia*.
 - (7)* Fruit tuberculate on the centre of each face, with smooth margins; pappus crown-shaped 8. Superspecies *trachycarpa*.

7. Superspecies *iberidifolia*.

Key to the Species.

- (1). Pappus minute.
 - (2). Fruit broadly obovate and flat; margin irregularly and shortly lobed. Leaves cauline.
 - (3). Leaves pinnatisect, the segments mucronate 38. *B. Billardieri*.
 - (3)* Leaves entire or crenate 39. *B. Tatei*.
 - (2)* Fruit oblong-cuneate, turgid and slightly flattened; margin smooth.
 - (4). Much branched, more or less glandular herbs with cauline pinnatisect leaves 37. *B. iberidifolia*.
 - (4)* Small glabrous herbs with leaves mainly radical, entire, linear to broad-linear.
 - (5). Ray florets white. Fruit black, microscopically tessellated, glabrous, 0.9-1.1 mm. long, 0.5-0.6 mm. broad 41. *B. bellidioides*.
 - (5)* Ray florets blue. Fruit brown, smooth, with long apically rolled hairs distally, 1.8 mm. long, 0.9 mm. broad 42. *B. pusilla*.
- (1)* Pappus absent. Leaves radical and cauline.
 - (6). Leaves entire or pinnatisect. Fruit cuneate, flat and glabrous, with smooth margins 40. *B. parvula*.
 - (6)* Leaves pinnatisect. Fruit clavate. Shouldered, with curled glandular hairs present distally 43. *B. exilis*.

8. Superspecies *trachycarpa*.

Key to the Species.

- (1). Fruit not dimorphic.
 - (2). Fruit narrow-oblong-cuneate, flattened, wingless, tuberculate with smooth margins, 1.5-1.8 mm. long, 0.6-0.8 mm. broad. Pappus minute and coroniform. Leaves often entire and canaluculate, with a few small leaves arising from the axils 44. *B. trachycarpa*.
 - (2)* Fruit obovate, flat, with entire or irregularly dissected wings, 2.2-2.9 mm. long, 1.1-1.5 mm. broad; the body smooth and pappus well developed. Leaves pinnatisect and crowded 45. *B. rigidula*.

- (1).* Fruit dimorphic, those of the rays wingless, narrow-oblong cuneate and slightly flattened, tuberculate with smooth margins and short pappus. Disc fruits flat, obovate, the body not tuberculate, the wings broad, and the pappus slightly larger than in the ray fruit 46. *B. ciliaris*.

9. Superspecies *ciliocarpa*.*Key to the Species.*

- (1). Fruit wingless, with long glandular hairs. Involucral bracts obovate with obtuse to subacute apices.
 (2). Fruit oblong-cuneate and flattened, with glandular hairs on the centre of each face and along the outer edge of each margin 47. *B. ciliocarpa*.
 (2).* Fruit laterally compressed and shouldered distally, with glandular hairs only on the flattened face and summit of the smooth margins 48. *B. oncocarpa*.
 (1).* Fruit with narrow and irregularly dissected wings; body proximally flattened and distally dilated. Involucral bracts lanceolate with a filiform apex 49. *B. cheilocarpa*.

10. Superspecies *latisquamea*.

Erect woody perennials with a thick tap-root. Leaves cauline, lanceolate, entire and sessile. Involucral bracts often in three rows. Fruit up to 3.5 mm. long, 2.5 mm. broad, obovate, and surrounded by an entire wing. Pappus ring-like, with minute and irregular teeth 50. *B. latisquamea*.

11. Superspecies *Silphiosperma*.*Key to the Species.*

- (1). Densely glandular-hairy branching annuals with pinnatisect leaves. Fruit up to 3 mm. long, 1.8 mm. broad, flat and slightly curved, with smooth and entire margins 51. *B. glandulosa*.
 (1).* Glabrous to sparsely glandular-pilose annuals often unbranched, with entire to pinnatisect leaves. Fruit 2.2-2 mm. long, 1.1-1.5 mm. broad, flat, the margins broad, wing-like and deeply dissected 52. *B. perpusilla*.

DESCRIPTIONS OF SPECIES.

Subgenus EUBRACHYCOME.

1. Superspecies TENUISCAPA.

1. BRACHYCOME TENUISCAPA Hook. f.

Erect stoloniferous perennials up to 26 cm. high, with a glandular-septate indumentum. Leaves radical, oblanceolate to ovate-cuneate, dentate to almost crenate distally, with sheathing bases. *Scapes* erect, 1-6, rather robust, bearing 1-3 leaves. *Capitula* up to 1 cm. diameter. *Involucral bracts* 16-22, 4-5 mm. long, 1.6-2 mm. broad, broad-linear to narrow-oblong, glandular, obtuse to subacute, with microscopically serrulate margins. *Ray florets* up to 60, rays 7 mm. long, 1.4 mm. broad, mauve. *Receptacle* up to 1.8 mm. broad, 1.5 mm. high, steeply conical, moderately pitted. *Fruit* 1.2-1.8 mm. long, 0.9 mm. broad, cuneate, flattened, dark-brown to black, thickened marginally, otherwise smooth. Pappus short, white.

Key to the varieties.

- (1). Leaves usually somewhat fleshy and forming a basal rosette, up to 3 cm. long, 6 mm. broad. Fruit dark brown var. *a tenuiscapa*.
 (1).* Leaves rather rigid and macroscopically hairy, up to 10.5 cm. long, 1.8 cm. broad; dead remains of previous leaves persisting as fibrous strands around the base of the plant. Fruit black var. *β pubescens*.

Brachycome tenuiscapa Hoof. f., var. *a tenuiscapa* comb. et stat. nov.

Lond. Jour. Bot., vi (1847), 114.

(Text-figs. 3, 8; Plate vi, map 1.)

Synonymy: *B. scapiformis* DC. var. *tenuiscapa* Benth, *Fl. Aust.*, iij (1866), 517. *B. alpina* Morris, *Vic. Nat.*, xli (1924), 31.

Type Locality: Middlesex Plains, Tasmania, Gunn. All syntype material at the Herbarium of the Royal Botanic Gardens, Kew.

Leaves distally toothed or almost crenate, up to 3 cm. long, 6 mm. broad, forming a basal rosette. *Scape* single, bearing 1-3 leaves, the uppermost linear to oblanceolate, entire, subacute to acute, the lower toothed distally and similar to the radical leaves, though smaller. *Ray florets* up to 33. Fruit dark brown.

Range: Highlands of Victoria and Tasmania.

Specimens examined:

Victoria: Australian Alps, F. Mueller (MEL, NSW); Pretty Valley, Bogong Plateau, 1.1923, H. B. Williamson (lectotype and 5 lectoparatypes of *B. alpina* Morris, MEL).

Tasmania: Arthur's Lakes, 17.1.1845, Gunn n. 321 (haptotype of *B. scapiformis* var. *tenuiscapa* Benth., NSW); W. Tiers via Molle, 12, 1914, R. A. Black (RAB).

Although authentic syntype material is not available in Australia, Hooker's description of *B. tenuiscapa* is such that no doubt exists as to the correct application of the name. A haptotype of *B. scapiformis* var. *tenuiscapa* has been nominated and used as a basis of comparison, this specimen agreeing satisfactorily with Hooker's description. Hooker clearly states that the fruit are wingless, but Bentham (1866) remarks "in some specimens the immature achenes show no wings, in others they are certainly winged". This apparent variability in one of the few stable characters of this genus is explained on the assumption that Bentham had before him specimens of *B. tenuiscapa* and a small form of *B. aculeata*. These are vegetatively identical and unless fruits are present of sufficient maturity to show the presence or absence of a wing, exact determination is impossible. Fortunately indications of a wing make their appearance early in development. Following his description of *B. alpina* Morris states that "superficially the plant resembles a small form of *B. scapiformis* DC. which has winged achenes". Lectotype and lectoparatypes of *B. alpina* have been nominated, but the name itself relegated to synonymy.



Text-figures 3-7. Habit studies. $\times \frac{1}{2}$.

3. *B. tenuiscapa* (Haptotype of *B. scapiformis* var. *tenuiscapa*). 4. *B. tenuiscapa* var. *pubescens*. 5. *B. scapigera*. 6. *B. decipiens*. 7. *B. Stuartii*.

Brachycome tenuiscapa Hook. f., var. β *pubescens* (Benth.), n. comb.
(Text-fig. 4; Plate vi, map 1.)

Synonymy: *B. decipiens* Hook f., var. *pubescens* Benth., *Fl. Aust.* iii (1866), 517.

Haptotype: *New England, C. Stuart (NSW).

Homeotype: Armidale, New England, "Hillside, forest", 9.11.1941, G. L. Davis (NSW).

Leaves dentate distally, up to 10.5 cm. long, 1.8 cm. broad, macroscopically hairy. *Scapes* 1-6, each bearing a more or less median bract. *Ray florets* usually 50-60. *Fruit* black.

Habitat: Open forest land in well-drained situations.

Range: Southern Queensland to Ballarat, through highlands of New South Wales, with a single record from Tasmania.

Specimens examined:

Queensland: Stanthorpe, 12.1875, 6.11.1890, F. M. Bailey (BRI).

New South Wales: Bolivia, 4.11.1886, E. Bêche (NSW); *Torrington, 29.9.1907, R. H. Cambage (NSW); *Glen Innes, 6.1917, J. L. Boorman (NSW); *Glen Innes, 3520' "In partial shade of *Eucalyptus* in closely grazed paddocks of cleared Euc. forest country, on median and heavy brown soils, amongst grasses", 8.4.1931, C. E. Hubbard (BRI); Dumaresq Crk., Armidale, "Forest land", 23.11.1941, Consett Davis (BRI, NSW); Armidale, "hillside, forest land", 19.11.1941, G. L. Davis (NSW, Homeotype; MEL, BRI, AD, HO, PERTH); *Uralla, 3.1912, A. McNutt (NSW); *New England, C. Stuart (NSW, haptotype; MEL); *Walcha Road, 24.10.1886, E. Bêche (NSW).

Victoria: *Ballarat (MEL).

Tasmania: Creek at foot of Mt. Wellington, 12.1870, S. Hannaford (MEL).

Originally described as a variety of *B. decipiens*, the size and glabrous nature of the fruit indicate that this population is more closely allied to *B. tenuiscapa*, with which species it is now combined. Syntype material of *B. decipiens* var. *pubescens* is at Kew, and consequently has not been examined, but a specimen bearing the type caption "New England, C. Stuart" has been nominated haptotype. Unfortunately this specimen is a flowering one, so it was considered desirable to select a fruiting homeotype. This variety can be readily identified on sight by the rather stiff, distally-toothed leaves, which have a harsh feeling, and the presence of the fibrous remains of former leaves round the base of each plant.

Variation is slight and confined to the indumentum, the hairs of which, though visible macroscopically, may occasionally be considerably shorter.

2. BRACHYCOME SCAPIGERA (Sieb. ex Spreng.) DC.

Prod. VII, (1838), 277.

(Text-figs. 5, 9; Plates vi, map 2; vii, 1.)

Synonymy: *Senecio scapigera* Sieb. ex Spreng. Syst. iii (1826), 559. *Brachystephium scapigerum* (Sieb. ex Spreng) DC., Prod. vi (1837), 304.

Lectotype: "Fl. Novae Holl. No. 332, 1825, Mr. Sieber" (GENEVA).

Erect glabrous perennials up to 40.5 cm. high, the bases of which bear the dead remains of former leaves. Leaves radical, up to 19 cm. long, 1.5 cm. broad, linear to oblanceolate, acute, entire, basally attenuate. *Scapès* 1-6, usually with 2 small bract-like leaves, but occasionally more. *Capitula* up to 1.2 cm. diameter. *Involucral bracts* about 18, up to 5 mm. long, 3 mm. broad, oblanceolate, obovate to broad elliptical, usually obtuse, rarely subacute, glabrous or microscopically glandular. *Ray florets* 30-50, the rays up to 9 mm. long, 2 mm. broad, white or mauve. *Receptacle* up to 3 mm. broad, 1 mm. high, conical, moderately pitted. *Fruit* 2.3-3 mm. long, 0.8-1.2 mm. broad, cuneate, brown, flattened, with narrow, thickened, smooth margins. Pappus short.

Habitat: Open forest land, frequently occurring on swampy ground.

Range: Southern Queensland, tablelands and south coast of New South Wales, through highlands of Victoria to the Grampians.

Specimens examined:

Queensland: *Stanthorpe, H. Tryon (BRI).

New South Wales: Jennings, 12.1903, J. H. Maiden and J. L. Boorman (NSW); *Glen Innes, 11.1911, F. H. Kenny (BRI); *Glen Innes, 1.1914, H. M. R. Rupp (NSW); Mt. Mitchell, near Guyra, 23.3.1941, G. L. Davis (NSW, BRI, MEL); *Rose Hill, Guyra, "forest land", 24.2.1941, G. L. Davis (NSW); 10 miles S.E. Guyra, "swampy ground", 18.2.1941, G. L. Davis (BRI); Yarooma, "swampy ground", 31.1.1941, G. L. Davis (NSW, MEL); Jeogla, "cleared grassland, slightly swampy", 5.3.1942, Consett Davis (NSW); Moona plains, 11.1904, A. R. Crawford (NSW); Jenolan Caves, 12.1899, W. F. Blakely (NSW); *Wingello, 11.1899, J. L. Boorman (NSW); *Queanbeyan, 14.12.1911, R. H. Cambage (NSW); Bimberi Crk., Upper Cotter R., 6100', 15.1.1912, R. H. Cambage (NSW); O'Hara Head, between Milton and Bateman's Bay, 21.5.1939, F. A. Rodway (NSW); Kiandra, 12.1901, W. Forsyth (NSW); *beside Adaminaby-Talbingo Rd., <3000', 6.12.1943, S. Copland (NSW); *Kosciusko, "Treeline to 7000'", 1.1899, J. H. Maiden and W. Forsyth (NSW); Kosciusko, 12.1924, T. Harris (NSW).

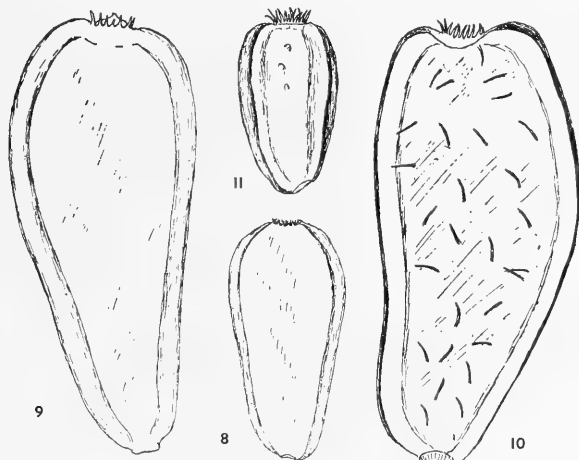
Victoria: *Australian Alps, F. Mueller (MEL); Cobboras Mts., 6000', 1.1854, F. Mueller (MEL, NSW); Buffalo Mts., 28.2.1853, F. Mueller (MEL); *Strathbogie, 11.1901, A. W. Vroland (NSW, MEL); Banks of the Delatite R., 3.1853 (MEL); *Mt. Stirling, 5700', "grassy summit", 4.1.1945, J. H. Willis (MEL); Mt. Painter, 2.1926, A. J. Tadgell (NSW); *Upper Yarra Ranges, 8.1900, C. Walter (NSW); *Eltham, 21.8.1903, P. R. H. St. John (MEL); Grampians, 11.1904, H. B. Williamson (BRI).

Sieber's specimen, now at Geneva, has been selected lectotype of this species as well as of *Senecio scapigera* and *Brachystephium scapigerum*, a lectoparatype being located at the Gray Herbarium, Harvard. Unfortunately both of these specimens, the only syntypes still extant, are in the flowering condition, but no doubt exists as to their identity. A photograph of the lectotype is here reproduced (Pl. vii, No. 1). Owing to the meagre data, no type locality can be given, but the specimen was probably collected somewhere in Victoria.

Intraspecific variation is slight and limited to the length:breadth ratio of the leaves and height of the plant. The maximum known height is exhibited in some specimens from Kiandra which reach 40.5 cm. and bear broad-linear leaves up to 19.5 cm. long and 4.5 cm. broad. Apart from these specimens, the greatest height was 29 cm. with leaves proportionally shorter.

No variation has been noted in the fruit, except in the case of a specimen from Jennings, in which they are all very turgid and there is a complete absence of pappus. Very young fruits on the same specimen, however, bear a minute pappus, so it is assumed that this was lost at maturity.

The fruits are very similar to those of *B. tenuiscapa* except in their consistently larger size, which, together with distinct vegetative features, warrants specific status, though the discontinuity between these two species is admittedly small.



Text-figures 8-11. Fruit. $\times 17$ approx.

8. *B. tenuiscapa*. 9. *B. scapigera*. 10. *B. decipiens*. 11. *B. Stuartii*.

3. BRACHYCOME DECIPIENS Hook. f.

Lond. Journ. Bot., vi, (1847), 114.

(Text-figs. 6, 10; Plate vi, map 3.)

Type locality: Lawrence, Tasmania, Gunn. All syntype material at the Herbarium of the Royal Botanic Gardens, Kew.

Glabrous perennials up to 21.5 cm. high. Leaves radical, up to 16.5 cm. long, 3.2 cm. broad, oblong-cuneate to elliptical, entire, shallowly crenate or acutely toothed distally, subacute to acute. *Scapes* 1-6, naked or with a single bract. *Capitula* up to 1.5 cm. broad. *Involucral bracts* about 24, up to 6.5 mm. long, 2.7 mm. broad, obtuse, broad-linear to narrow-obovate, entire, the margins usually purplish. *Ray florets* up to 40, the rays 8 mm. long, 2 mm. broad, bluish. *Receptacle* 7 mm. broad, 1.5 mm. high,

convex, moderately pitted. *Fruit* 3 mm. long, 1.4 mm. broad, cuneate, flattened, dark brown, with relatively long straight hairs on each surface, thickened marginally, each margin bearing a longitudinal groove almost at the edge. Pappus short.

Range: Southern highlands of New South Wales, through Victoria to the Adelaide district of South Australia. Widely distributed in Tasmania.

Specimens examined:

New South Wales: Birdsdale, near Braidwood, 9.1890, W. Bauerlen (N.S.W.); *Talbingo-Adaminaby Road, <3000', 6.12.1943, S. Copland (NSW); *Rule's Point, west of Kiandra, 26.11.1921, A. Forster (NSW); *Kiandra, 12.1901, W. Forsyth (NSW); Pretty Point, Mt. Kosciusko, 1.1899, J. H. Maiden and W. Forsyth (NSW).

Victoria: *Bogong Mts., 1.1923, H. B. Williamson (MEL); *Upper Genoa R., 9.1860, F. Mueller (MEL); Dargo Track, Mt. Bernard, 4000', 12.1914, A. J. Tadgell (MEL); *towards Dandenong Ra., 1.1853, F. Mueller (MEL); *Ringwood, 21.8.01, P. R. H. St. John (MEL); Plenty and Darebin Crks., "damp meadows", 10.1852, F. Mueller (MEL); Creswick, 10.1931, J. H. Willis (MEL); near Emu Creek and Wando Vale, 9.8.1943, J. G. Robertson (NSW); Hawkesdale, 10.1901, H. B. Williamson (NSW); *Hawkesdale, 11.1904, H. B. Williamson (BRI).

Tasmania: *Penquite, 27.8.1842, Gunn, n.511 (NSW); *Launceston, 7.9.1839, Gunn, n.511 (NSW); Launceston, 1866, R. C. Hannaford (NSW); *North Esk R., 29.9.1841, Gunn, n.511 (N.S.W.); *West Perth, F. Mueller (NSW); *near Perth, S. Hannaford (MEL); *George's Bay, R. Tate (AD); *Hampshire Hills (MEL); Surrey Hills, 20.11.1841 (MEL); *Macquarie Hb., 10.9.1842, Gunn, n.511 (NSW); *Mt. Direction, 12.11.1911, R. A. Black (RAB); *New Norfolk, 28.9.1840, 26.10.1840, Gunn, n.511 (NSW); *Mt. Nelson, 9.1892, 2.1893, L. Rodway (HO, NSW); Mt. Nelson, 5.9.10, 25.9.20, R. A. Black (RAB); *Sandy Bay, 10.1892, W. V. Fitzgerald (NSW).

South Australia: Brighton (MEL).

Syntype material of this species being at Kew, the author has been unable to make a personal examination of the specimens, and consequently type selection has not been possible. However, a number of specimens are available, collected in Tasmania by Gunn and others, which agree with Hooker's description, and it is on these specimens that the above description has been largely based.

Variation is apparent particularly in the leaf margins, and although the majority of specimens bear entire leaves, an appreciable number are either inconspicuously crenate distally or bear acute teeth in the same position. The leaves are apparently always thin and inclined to be flaccid, particularly the larger ones. The upper limits of leaf size were found in a specimen from Kiandra, but the majority do not exceed 7 cm. in length.

Even in the very young stages the fruit bear the straight hairs noted in the mature fruit, and for this reason they are a useful diagnostic character.

The purple margins to the involucrel bracts are a constant feature of all specimens examined and consequently are noted in the general description. This character, however, does occur occasionally in other species and is probably due to physiological factors.

Apart from the straight hairs on the fruit, which are the most obvious distinguishing feature from those of *B. scapigera*, the margin shows an interesting departure from the usual thickened condition. At the extreme edge of the thickened margin a longitudinal shallow groove runs the entire length of the fruit, leaving a very narrow strip of tissue down each edge of the fruit. This strip, though microscopic, is broad in the following species, *B. Stuartii*, and, in the author's opinion, is the morphological forerunner of the wing of other species.

4. BRACHYCOME STUARTII Benth.

Fl. Aust., iii, (1866), 513.

(Text-figs. 7, 11; Plate vi, map 4.)

Lectotype: New England, C. Stuart, n.14 (MEL).

Lectoparatype: *New England, C. Stuart, n.14 (MEL).

Erect glabrous perennials with a tufted mode of growth. Leaves radical, forming a basal rosette, up to 9.5 cm. long, pinnatisect with segments up to 9.7 mm. long, 2 mm. broad, subacute to acute, entire, irregularly toothed or lobed, becoming smaller and finally filiform proximally. *Scapes* naked and exceeding the leaves. *Capitula* 6-8 mm.

in diameter, 1-10 present. *Involucral bracts* 14-25, 3-3.5 mm. long, 1-1.5 mm. broad, oblanceolate, obtuse, entire or minutely serrulate. *Ray florets* 40-80, the rays 5-8 mm. long, 1 mm. broad, white, mauve or pale blue. *Receptacle* 1.2-1.9 mm. broad, 1.9-2.2 mm. high, conical, deeply pitted. *Fruit* 0.9-1.7 mm. long, 0.5-0.9 mm. broad, dark brown to black, cuneate, thick and laterally flattened, the central region bearing a few tubercles and marked off by two conspicuous longitudinal folds leaving a smooth margin on each side. Pappus short, the bristles white, of unequal length.

Habitat: Swampy ground, often forming a dense covering.

Range: Southern Queensland to New England Tableland of New South Wales.

Specimens examined:

Queensland: *Stanthorpe, 12.1875, F. M. Bailey (BRI); Stanthorpe, 6.11.1890 (BRI); Stanthorpe, "growing in clumps in the bed of the river", 11.1904, J. L. Boorman (NSW); Ruby Creek, Stanthorpe, "in shallow sandy soil with outcrops of granite. Herb with thick tuft of radical leaves and a single erect flowering stalk. Ray florets mauve, disc florets yellow", 23.11.1946, S. L. Everist and L. J. Webb (BRI); Wybera, "in shallow soil on flat rock ledges", 13.10.1933, C. T. White, n.9347 (BRI); Darling Downs, Racecourse Creek, north-east of Wallangarra, "forming a carpet of rosettes in soil-bearing hollows in the granite on the hillsides; rays pale lilac", 29.1.1940, L. S. Smith, n.767 (BRI).

New South Wales: *Tenterfield, 31.10.1886, E. Betche (N.S.W.); Tenterfield, 30.12.1910, F. H. Kenny (BRI); Emmaville, 10.1901, 10.1911, J. L. Boorman (NSW); Howell, 6.1904, J. L. Boorman (NSW); Sydenham, Barraba district, 11.1913, H. M. R. Rupp (NSW); Guyra, "low plant, foliage carpet-like, flowers pale blue", 6.1917, J. L. Boorman (NSW); New England, C. Stuart "n.14" (MEL, lectotype, lectoparatype); New England, C. Stuart, "n.152, Mountains, 1000" (MEL); New England, C. Stuart, "n.204" and "n.264, Mountains" (MEL); Trunkay, 11.1918, J. L. Boorman (NSW).

The syntype series available consists of 5 specimens collected in New England by C. Stuart and examined by Bentham prior to publication of the original description. Only one of these bears mature fruit and consequently this was nominated lectotype, but unfortunately this specimen is badly pressed and the characteristic appearance is obscured. As a result it was considered advisable to figure one of the other syntype specimens instead (n.264, "mountains").

Members of this species show little variation in vegetative features and none in the fruit, which in view of the limited range is not surprising. The specimens collected at Guyra by J. L. Boorman are the only ones showing any departure from the typical leaf condition. In these the segments are filiform to narrow-linear and markedly irregular in size and position; some segments are entire while others are themselves irregularly pinnatisect.

This species is particularly interesting in that it shows, in the fruit, the continuation of a trend apparent for the first time in *B. decipiens*, that of the development of longitudinal grooves separating off a margin from a central region. In *B. Stuartii* these grooves have deepened and the central region adjacent to them develops into longitudinal folds at maturity. The margin itself has become relatively broad and is easily distinguished.

2. Superspecies LEPTOCARPA.

5. BRACHYCOME LEPTOCARPA F. Muell.

Trans. Phil. Soc. Vic., 1 (1855), 43.

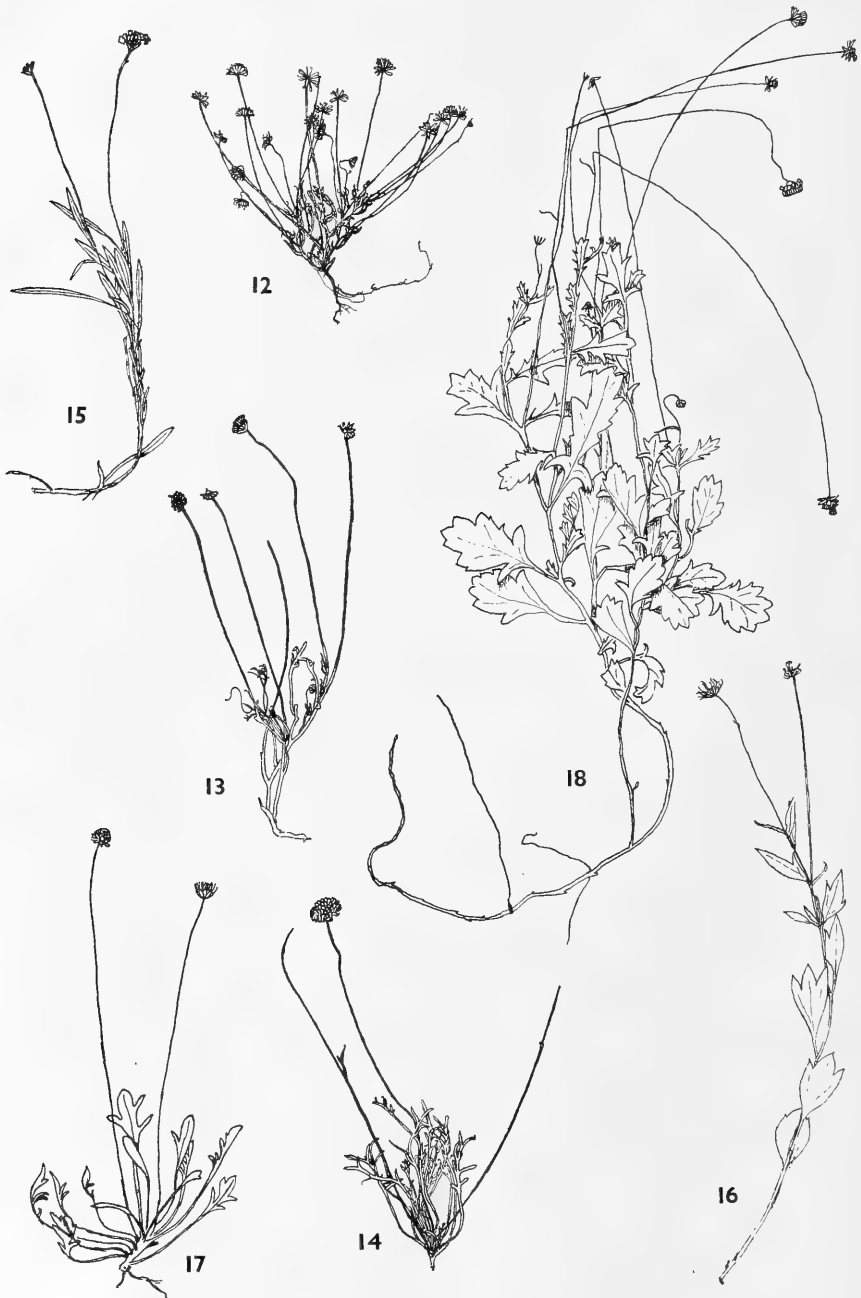
(Text-figs. 12, 23; Plate vi, map 5.)

Lectotype: Axe River, 11.1853, F. Mueller (MEL).

Lectoparatypes: Two. Axe River, 11.1853, F. Mueller (MEL).

Branching annuals, 2.5-26 cm. high, with an indumentum of glandular and septate hairs. Radical leaves linear, entire, acute, 1-3 cm. long, 0.5-1.2 mm. broad. Cauline leaves entire, toothed or pinnatipartite, up to 2.5 cm. long; segments linear, acute, up to 5 mm. long, 1 mm. broad. *Peduncles* naked. *Capitula* 4-7 mm. diameter, 1-30 present. *Involucral bracts* 15-26, 2.5-3 mm. long, 0.5-1 mm. broad, oblanceolate, glabrous or with a few glandular hairs on the outer surface, subacute to acute, with torn ciliate margins. *Ray florets* 15-18, the rays 3-4 mm. long, 1-1.2 mm. broad, white. *Receptacle* 1-1.3 mm. high, 1-1.2 mm. broad, steeply conical, unpitted. *Fruit* light brown to black, 1.5-2 mm.

long, 0.4–0.5 mm. broad, linear-cuneate, flattened, with smooth lateral margins, and long white distally-rolled hairs on the central area of each face. Pappus white, conspicuous, about one-quarter the length of the fruit.



Text-figures 12-18. Habit studies. $\times \frac{1}{2}$.

12. *B. leptocarpa* (Lectotype). 13. *B. debilis* (Haptotype). 14. *B. ptychocarpa* (Lectotype).
15. *B. angustifolia* var. *angustifolia*. 16. *B. angustifolia* var. *heterophylla* (Lectotype). 17. *B. dissectifolia* (Holotype). 18. *B. procumbens* (Holotype).

Habitat: Grassland.

Range: Central New South Wales, throughout Victoria to South-eastern South Australia.

Specimens examined:

New South Wales: *Wellington, 6.10.1886, E. Betche (NSW); *Stuart Town, 10.1911, L. Abrahams (NSW); Bowan Park, near Cudal, 10.1906, W. F. Blakely (NSW); between Griffith and Rankin Springs, 19.9.1938, D. O. Cross (NSW); Lachlan district, 1882, T. Duff (NSW); interior of N.S.W., C. Moore (MEL); River Darling, Victorian Expl. Expedition (MEL).

Victoria: Dry places on the Loddon, F. Mueller (MEL); You Yangs, 13.11.1910, H. B. Williamson (MEL); You Yangs, 4.1911, J. Staer (NSW); You Yangs, F. Mueller (BRI); Kamarooka, 3.10.1920, D. J. Paton (MEL); Bendigo, E. Semmers (MEL); McIvor, "Oct.", F. Mueller (MEL, NSW); Hilldene, 11.1942, Consett Davis (NSW, MEL); 2 miles N. of Longwood, 23.9.1942, Consett Davis (MEL); Longwood, 31.10.1936, R. A. Black (RAB); Axe R., 11.1852, F. Mueller (MEL, lectotype, lectoparatypes); 5 miles E. of Seymour, 11.1942, Consett Davis (NSW, MEL); 1 mile west of Seymour, 11.1942, Consett Davis (NSW, MEL); Darebin Crk., "with *Wahlenbergia gravillium pentamera*", 10.1852, F. Mueller (MEL); Port Melbourne, 1852, Hildebrandt (MEL); Co. Talbot, 10.1909, F. M. Reader (MEL); between Mt. Emu and Hopkin's Rivers, F. Mueller (MEL); Dunkeld, 9.11.1903, H. B. Williamson (NSW, BRI); Shire of Borung, 30.8.1903, F. M. Reader (MEL); Shire of Dimboola, 14.10.1894, 6.10.1895, 16.9.1898, F. M. Reader (MEL); Nhill, 4.1911, J. Staer (MEL); Wimmera, "black soil plains", 19.10.1938, A. Swaby (JMB); Jeparil, 20.9.1898, H. B. Williamson (MEL).

South Australia: Patawalonga Crk., Pt. Lincoln, L. Hamilton (JMB); Warren's Gorge, near Quorn, "on stony ground above creek", 2.10.1916, J. M. Black (JBC); Wirrabara, 10.1882, R. Tate (AD); S.Y.P., 11.1889, R. Tate (AD); Yarcowie, 10.10.12, M. Mills (JMB); Lofty Range; F. Mueller (MEL); Tanunda, F. Mueller (MEL), Barossa Range, 9.1848, F. Mueller (MEL); near Stringybark, Forrest Range, 12.10.1946, J. B. Cleland (JBC); Clarendon, "5th Nov.", O. Tepper (MEL); Strathalbyn, 2.10.1906, 6.10.1910, J. M. Black (JMB); Kensington, 11.1848, F. Mueller (MEL); Waterfall Gully, 10.1878, R. Tate (AD); Tintinarra, 10.1911, J. M. Black (JMB); Reedy Crk., 1848, F. Mueller (MEL); Lake George, R. Tate (AD); Lake Bonney, 1887, H. E. Wehl (MEL).

No specific type locality being recorded by Mueller in the original description ("In low grassland, not infrequent in the colony of Victoria, as well as in South Australia"), a syntype series was selected consisting of three specimens from the Axe River, collected by Mueller himself two years prior to publication of this species. From this series a lectotype was selected, and the remaining two specimens become lectoparatypes. *B. leptocarpa* was listed by Bentham (1866) as a synonym of *B. exilis*, but the two species are quite distinct in every way. The issue was further confused by the fact that when he redescribed *B. exilis*, Bentham had before him specimens which have been traced and identified as *B. leptocarpa*. As a result, his description applies to the latter species and not to *B. exilis*, under which name it appears. This mistake has been faithfully perpetuated in all subsequent Australian floras.

The differences noted in the relatively large series available of this species are to be correlated with the size of the plants concerned. In the case of dwarf specimens 2.5-5 cm. high, the leaves are usually entire or minutely toothed, with a single peduncle, which may rise from a basal cluster of leaves so that no stem is present. With increase in size of the plant a branching stem is found, and as a result there is an increase in the number of inflorescences. No structural variation has been observed in the fruit. Unless reasonably mature fruits are present, *B. leptocarpa* cannot be distinguished from *B. debilis*, both species agreeing in all vegetative characters. It is not until the presence or absence of a wing on the fruit can be established that a reliable identification can be made. These two species frequently coexist in the same situation, without, apparently, any hybridization occurring.

6. BRACHYCOME DEBILIS Sond.

Linnaea, xxv (1852), 477.

(Text-figs. 13, 24; Plate vi, map 6.)

Haptotype: Kensington, St. Vincent's Gulf, 11.1848, F. Mueller (MEL).

Septate-hairy and sparsely glandular branching annuals up to 11.8 cm. high. Lower cauline leaves up to 1.8 cm. long, pinnatisect, with 3-7 acute distal lobes up to 5 mm. long, 0.8 mm. broad, rarely entire and linear; upper leaves usually linear and entire. Radical leaves up to 1 cm. long, narrow linear, entire, only present in small specimens

and soon disappearing. *Peduncles* naked, glandular proximally. *Capitula* 1-6, 4-8 mm. diameter. *Involucral bracts* about 18, 2-2.6 mm. long, 0.6-0.8 mm. broad, obtuse to subacute, narrow-obovate with torn-ciliate margins. *Ray florets* 13-18, the rays 4 mm. long, 0.9 mm. broad, white. *Receptacle* 1-1.5 mm. broad, 1-1.5 mm. high, steeply conical. *Fruit* about 2 mm. long, 1 mm. broad, flat, obovate, the body brown and glabrous or bearing a few glandular hairs. Wings entire, shallowly or deeply dissected with short glandular hairs on the margin. Pappus conspicuous.

Range: This species seems rather localized in its distribution, and, with the exception of a single record from New South Wales, is confined to the central region of Victoria and south-eastern South Australia. Whether its natural limits are more extensive can only be determined by further collecting.

Specimens examined:

New South Wales: South Ita, 19.9.1925, A. Morris (NSW).

Victoria: You Yangs, F. Mueller (BRI); 5 miles east of Seymour, 11.1942, Consett Davis (NSW, MEL); 1 mile west of Seymour, 11.1942, Consett Davis (MEL).

South Australia: Glenelg, St. Vincent's Gulf, F. Mueller (MEL); Marino, near Old Well, "cliffs", 23.10.10, H.H.D.G. (JMB); Kensington, 11.1848, F. Mueller (MEL, Haptotype); Waterfall Gully, 4.10.1942, J. B. Cleland (JBC); Robe, 28.9.13, J. M. Black (JMB); S.E., "dry land, Ti-Tree Association" R.L.C., 11.1939, n. 4189 (AD).

Attempts to trace authentic syntype material of this species having failed, a haptotype was selected, which will become the neotype if it is established that Sonder's own specimens are no longer extant.

The small series of specimens available shows little variation in general appearance except in size and associated characters, which are probably to be correlated with habitat. The specimens from Seymour were found growing in a wet situation which, as summer progressed, became dried out and no further specimens were found. In such a situation it is necessary for the plants to grow from fruit of the previous season, and, in a relatively few weeks, to mature sufficiently to set seed themselves. It is not surprising under these circumstances that the plants are small and delicate, the smallest measuring 4.5 cm. in height. The maximum height recorded is attained by the haptotype, which is relatively robust, indicating a longer growing period. The only variation exhibited by the fruit is that of the margin of the wing. Although the fruits of the haptotype bear entire wings, the usual condition is for them to be more or less dissected, but the series of specimens is too small to permit any generalizations being put forward.

The specimens from Seymour were growing intermixed with others of *B. leptocarpa*, these two species being vegetatively identical. In this connection it is interesting to note that Mueller also collected both species from Kensington (11.1848), but whether they were in association or not is unfortunately not recorded.

The vegetative resemblance of *B. debilis* and *B. leptocarpa* is so close that identification cannot be certain in the absence of fruit, at least approaching maturity. This similarity is thought to be based on a close phylogenetic relationship, since it is noted also in the fruit. In the shape of the body, presence of glandular hairs, and characters of the pappus, there is little to distinguish the fruit of these two species. However, *B. debilis* shows a distinct advance over the *leptocarpa* type of fruit in the development of a wing which is one of the tendencies apparent in this superspecies.

7. BRACHYCOME PTYCHOCARPA F. Muell.

Trans. Phil. Soc. Vic., 1 (1855), 43.

(Text-figs. 14, 25; Plate vi, map 6.)

Lectotype: Buffalo Range, 26.2.1853, F. Mueller (MEL).

Glabrous annuals up to 15.5 cm. high, with a basal cluster of pinnatisect leaves up to 6 cm. long, including the petiole. Segments 5-8, up to 6 mm. long, 1 mm. broad, linear, acute. *Scapes* 1-6, filiform, naked or with a single entire or pinnatisect bract. *Capitula* 4-6 mm. diameter. *Involucral bracts* 12-15, 2-3.5 mm. long, 1-1.5 mm. broad, obovate, obtuse to subacute, microscopically torn-ciliate. *Ray florets* 25-70, the rays 2.5-3.5 mm. long, 0.8-1 mm. broad, "pink". *Receptacle* 1.2-2.5 mm. broad, 1.6-2.9 mm. high, steeply conical, moderately pitted. *Fruit* 0.9-1.1 mm. long, 0.6-0.8 mm. broad, obovate, brown; body flattened, with three longitudinal ridges on each side, the outer

microscopically serrated, the central one bearing a few glandular hairs; wings relatively broad with short marginal glandular hairs. Pappus of moderate length.

Range: Highland districts from Mt. Macquarie to Strathbogie ranges.

Specimens examined:

New South Wales: Mt. Macquarie, near Carcoar, 12.1907, J. L. Boorman (NSW); Quartzville to Neuminemang, "pink", W. Forsyth (NSW).

Victoria: Buffalo Range, 26.2.1853, F. Mueller (MEL, lectotype); Strathbogie Ranges, 11.1901, A. W. Vroland (MEL); Strathbogie, 12.1903, A. W. R. Vroland (NSW, BRI),

Owing perhaps to the short series available of this rare species, no variation was noted. The fruits are very distinctive in their small size with relatively broad wing and large pappus. The body, which is longitudinally grooved, is sharply demarcated from the wing, a character which places it in the *leptocarpa* group, but otherwise its natural affinities are obscure. In habit and the possession of pinnatisect leaves, a similarity does exist to certain small specimens of *B. nivalis*, but this in the author's opinion is purely superficial with probably an ecological basis.

8. BRACHYCOME ANGUSTIFOLIA A. Cunn. ex DC.

Prod. v (1836), 306.

Ascending stoloniferous perennials, up to 35 cm. high, glabrous or glandular-hairy, freely branching. Leaves cauline, up to 5.3 cm. long, 9 mm. broad, narrow lanceolate to elliptical, entire or irregularly pinnatifid, with prominent midvein. Lower leaves often sessile, the upper usually more or less petiolate. *Peduncles* filiform, naked or occasionally with a distal bract. *Capitula* up to 9, about 5 mm. diameter. *Involucral bracts* about 14, 2.1-3 mm. long, 0.5-0.9 mm. broad, linear to narrow-oblongate, acute, glandular, more or less torn-ciliate. *Ray florets* 13-29, the rays 6-10 mm. long, 1-3.5 mm. broad, pink, mauve or blue. *Receptacle* about 2.3 mm. broad, 1.5 mm. high, convex, shallowly pitted. *Fruit* 2-2.2 mm. long, 0.9 mm. broad, brown, narrow-cuneate, flattened, conspicuously tuberculate on each face, the margins smooth, narrowly winged. Pappus conspicuous.

Key to the varieties.

- (1). Leaves narrow-lanceolate to narrow-elliptical, entire var. *a angustifolia*.
 (1)* Leaves narrow- to broad-elliptical, pinnatisect var. *β heterophylla*.

Brachycome angustifolia A. Cunn. ex DC. var. *a angustifolia* comb. et stat. nov.

(Text-figs. 15, 26; Plates vi, map 7; vii, 2.)

Synonymy: *B. linearifolia* DC., Prod. v (1836), 306.

Lectotype: *Goulburn Plains, 5.1824, A. Cunningham (MEL).

Glabrous perennials, sometimes with an ascending habit. Leaves always entire with acute apices, narrow-lanceolate to narrow-elliptical.

Habitat: Relatively common in hind-dune forest in eastern Australia, otherwise in forest-land.

Range: Coast and tablelands of New South Wales southward from the Hawkesbury River; north-eastern and south-western Victoria to south-eastern South Australia; north-eastern and central regions of Tasmania.

Specimens examined:

New South Wales: Wiseman's Ferry, 4.1908, J. L. Boorman (NSW); Katoomba, Federal Pass, 2.500', 1.1904, W. A. Dixon (NSW); Burragorang to Wentworth Falls, 10.1898, J. H. Maiden (NSW); Blue Mts., 2.1.1887, J. J. Fletcher (NSW); *Parramatta, F. Mueller (MEL, NSW); Parramatta, 11.1884, E. Betche (NSW); Gordon-Pymble, "dry gravelly soil", 4.1914, W. F. Blakely (NSW); Northern Suburbs Cemetery, Sydney, 7.6.1927, E. Cheel (NSW); Ryde, 5.1887, R. T. Baker (BRI); Ryde, 4.1914; A. A. Hamilton (NSW); Cronulla, beach, 6.09, A. A. Hamilton (NSW); Cronulla, Eucalypt forest, G. L. Davis (NSW); Woonona, "cleared shrub dune, 20'", 1.6.1941, Consett Davis (NSW, BRI, MEL, AD, HG, PERTH); Corrimal, "open hind-dune forest", 4.9.1940, H. S. Browne (NSW); Bowral, 2.1906, R. H. Cambage (NSW); near Goulburn R., 4.1850 (MEL); *Goulburn Plains, 5.1824, A. Cunningham (MEL, Lectotype); Jenolan Caves, 10.1899, W. F. Blakely (NSW).

Victoria: *Morass Crk., Benambra, 5.1.1922, H. B. Williamson (MEL); *Lorne, 1.1922, A. C. F. Gates (MEL); Portland, near swamps (MEL); *Priest Point, Glenelg R. (MEL); Nelson, 5.1.1908, J. M. Black (BL); Glenelg R., mouth, W. Allitt, H. B. Williamson (MEL).

Tasmania: Fingal, 9.1.1914, R. A. Black (RAB); *near Lake St. Clair, 1,000', 8.2.1945, W. M. Curtis (HO); Tasmania, Gunn, n. 266 (NSW).

South Australia: Gawler R., near Tanunda, 15.4.1848, F. Mueller (MEL); *Mallee Scrub, F. Mueller (MEL); Murray R., 10.1848, F. Mueller (MEL); *Cape Northumberland, in lagoon, 16.11.1882, R. Tate (AD).

It is unfortunate that the only syntype of Australia should be a flowering specimen. This was nominated lectotype, there being no doubt as to its identity, and it has been satisfactorily matched with a number of complete specimens whose fruits agree with Cunningham's description.

It is not clear from De Candolle's description in what way he considered *B. linearifolia* to be a distinct species. The only comment made about the fruit in the original description is: "the fruits are crowned with a pappus like the preceding species" (that is, like *B. angustifolia*), and his description of the vegetative characters applies equally well. The author is indebted to Professor Baehni of Geneva for a photograph, fruit and florets of De Candolle's syntype specimens ("New Holland, 1816, Lambert", and "New Holland, Thiband"), which show conclusively that De Candolle's *B. linearifolia* is conspecific with *B. angustifolia*. Since both these species were described in the same publication, neither has priority, so the name *B. angustifolia* is retained, being that in current use. The syntype specimen collected by Lambert is nominated lectotype, and that of Thiband, lectoparatype of *B. linearifolia*.

The only variation of any significance was shown by specimens from South Australia ("Gawler R." and "Mallee Scrub") in which the plants are erect and not ascending. Otherwise in all specimens examined variation was limited to small differences in the size of the leaves, and in one specimen ("Wiseman's Ferry"), one or two small teeth are present on some leaves.

Vegetatively this species shows a very strong resemblance to *B. graminea*, so that in certain flowering specimens difficulty is experienced in identification. The leaves of *B. angustifolia* are somewhat stiffer than those of *B. graminea*, and if any trace of a pappus can be found on even very young fruits, it is reasonably safe to identify the specimen as the former species. The wing and tubercles on the fruit only make their appearance at maturity, and as the pappus bristles break off readily, old fruit commonly appear to have a very short pappus.

A definite natural affinity appears to exist between *B. angustifolia* and *B. leptocarpa*, though considerable advances are shown in the fruit of the former species, which although of the same shape, is larger, and considerably thicker, while the development of the wing is a new character. It has been observed that the tubercles of the mature fruit of any species are represented in the young stages by curled glandular hairs. It is considered that this sequence is a phylogenetic one and that plants with tuberculate fruits developed from ancestors possessing fruits bearing this type of hair.

Brachycome angustifolia A. Cunn., ex DC., var. *heterophylla* (Benth.) comb. nov.

(Text-fig. 16; Plate vi, map 7.)

Synonymy: *B. heterophylla* Benth., Enum. Pl. Hueg., 1 (1837), 50; *B. linearifolia* DC., var. β , *heterophylla* (Benth.) Moore and Betche, Fl. N.S.W. (1893), 264.

Lectotype: Australia, 1802-5, R. Brown (MEL).

Lectoparatypes: Five, *Australia, 1802-5, R. Brown (MEL).

Shortly glandular-hairy perennials, with narrow- to broad-elliptical, pinnatisect leaves; lobes of leaves 1-5, acute, distally placed. Lowest leaves often entire.

Range: Central coastal area of New South Wales through Liverpool Plains district to Queensland border.

Specimens examined:

New South Wales: Emmaville, 2.1911, F. H. Kenny (BRI); Howell, 8.1905, J. H. Maiden and J. L. Boorman (NSW); Howell, 6.1904, J. L. Boorman (NSW); Tingha, 16.10.1903, R. H. Cabbage (NSW); Warrumbungle Ranges, 10.1899, 10.1901, W. Forsyth (NSW); *Timor Rock, Coonabarabran, 9.1908, J. L. Boorman (NSW); Coonabarabran, 10.1916, J. L. Boorman (NSW); Tamworth, 11.1904, H. M. R. Rupp (NSW); Murrurundi, 1.10.1907, R. H. Cabbage (NSW); Pokolbin, "rays blue", 4.1906, R. H. Cabbage (NSW); Stewart's Brook, 8.1899, J. H. Maiden (NSW); Newcastle, 8.1897, J. H. Maiden (NSW); Newcastle, 4.10.1911, A. A. Hamilton (NSW); Australia (? Port Jackson), 1802-5, R. Brown (MEL).

The syntype series consists of six specimens presented to the National Herbarium, Melbourne, by the British Museum in 1876, several years after the publication of Bentham's description of *B. heterophylla*. Although further syntype specimens are at Kew, Bentham also examined Brown's specimens at the British Museum, and it is therefore reasonable to assume that these specimens are authentic syntypes. One of them was accordingly selected lectotype both of *B. heterophylla* Benth. and *B. angustifolia* var. *heterophylla*, and the remainder nominated lectoparatypes of both names.

Variation in the shape of leaves is considerable, and the margins may be irregularly or regularly dissected. The fruits are essentially the same throughout the series examined, but the narrow thin wing is not always apparent, possibly due to immaturity.

9. BRACHYCOME DISSECTIFOLIA SP. NOV.

(Text-figs. 17, 27; Plate vi, map 8.)

Holotype: Ten miles south-east of Guyra, "swampy ground", 18.2.1941, G. L. Davis (NSW).

Paratypes: Three, l.c. (MEL, BRI, AD).

Herba perennis, erecta aut adscendens, stolonifera, ad 17 cm. alta, pilis paucis longis in basi foliorum neglectis glabra; folia radicalia ad 6.5 cm. longa, oblanceolata, vel integra, vel acute 1-3 dentata, dentibus 1-9 lobis subacuminatis-acuminatis obovato-lanceolatis ad 5 mm. longis, 1.7 mm. latis saepe pinnatisectis, interdum pinnatifidis. *Pedunculi* filiformes, glabri, fere folio basi uno integro nudi. *Capitula* 1-5, circiter 5 mm. transverse lata. *Involucri phylla* 14-18, ad 2.8 mm. longa, 1.9 mm. lata obovata, obtusa, glabra, mic. serrata. *Flores radii* circa 34, ad 4 mm. usque longi, 1.1 mm. lati, violacei aut albi. *Receptaculum* 2 mm. latum, 1.5 mm. altum, hemisphaericum. *Achaenia* 1.5 mm. longa, 1 mm. lata, fusca-nigra, late obovate-cuneata, corpore ab ala acute secto, marginibus elevatis, in disco tuberculato; ala corpore dimidio angustiora, integra, pilosa, pilis margine brevibus, rectis, albis. Pappus setis, albis, mediocriter longis.

Erect or ascending stoloniferous perennials up to 17 cm. high, glabrous except for a few long septate hairs at the leaf bases. Leaves radical, up to 6.5 cm. long, oblanceolate and entire, or with 1-3 acute teeth, frequently pinnatisect with 1-9 sub-acute to acute obovate-lanceolate lobes up to 5 mm. long, 1.7 mm. broad, occasionally pinnatifid. Scapes filiform, glabrous, naked except for a single filiform entire leaf proximally. *Capitula* 1-5, about 5 mm. in diameter. *Involucral bracts* 14-18, up to 2.8 mm. long, 1.9 mm. broad, obovate, obtuse, microscopically serrulate, glabrous. *Ray florets* about 34, up to 4 mm. long, 1.1 mm. broad, mauve or white. *Receptacle* 2 mm. broad, 1.5 mm. high, hemispherical. *Fruit* 1.5 mm. long, 1 mm. broad, dark brown to black, broadly obovate-cuneate, the body sharply demarcated from the wing, raised at the margins and centrally tuberculate; wing about half the breadth of the body, entire with short straight white hairs at the margin. Pappus of white bristles of moderate length.

Habitat: In New England this species is found in abundance in roadside ditches and around the margins of swamps.

Range: Northern tablelands of New South Wales, and coast at Port Stephens.

Specimens examined:

Mt. Lindsay, 4.1914, H. M. R. Rupp (NSW); Inverell Rd., 7 m. west of Guyra, 18.2.1941, G. L. Davis (BRI, NSW); Rose Hill, Guyra, "Swampy ground, rays mauve", 24.2.1941, G. L. Davis (BRI, NSW, MEL); 5 m. from Guyra on Baldersleigh Road, "rays white to pale mauve", 23.3.1941, Consett Davis (NSW, MEL); 10 m. south-east of Guyra, "Swampy ground, rays white", 18.2.1941, G. L. Davis (Holotype NSW; paratypes MEL, BRI, AD); Booroolong Creek, New England, "Swampy ground beside creek", 18.2.1941, G. L. Davis (NSW, MEL); Port Stephens, "Sand dune, rays mauve", 4.9.1941, Consett Davis (BRI, NSW, MEL).

The marked variation in the leaves is one of the most striking features of this species, entire, toothed and even pinnatisect leaves being frequently noted on the same plant. The lobes are usually irregularly arranged, but in one specimen ("7 m. west of Guyra") the leaves are regularly pinnatisect and similar in appearance to those of *B. Stuartii*.

The body of the fruit is sharply demarcated from the wing and smooth slightly raised margins are present, while the presence of a narrow band of small tubercles is an advance on the "*debilis*" type.

Apart from the tubercles, the resemblance of the fruit to those of *D. debilis* is close, glandular hairs having apparently given place to tubercles, and being no longer present at maturity.

10. BRACHYCOME PROCUMBENS SP. NOV.

(Text-figs. 18, 28; Plate vi, map 8.)

Holotype: Blue Hole, near Armidale, "Rocky situations on steep slopes among boulders", 15.4.1941, Consett Davis (NSW).

Paratypes: Two l.c. (MEL BRI).

Herba perennis, ad 34.5 cm. alta, glabra, stolonifera; caulis e basi ramosissimus adscendens aut procumbens. Folia caulina, petiolo gracili non neglecto, pleraque ad 6 cm. longa, grosse pinnatifida-pinnatipartita, lobis circiter 7 ad 9 mm. longis, 4 mm. latis, cuneatis, acuminatis, saepe mucronatis. Folia inferiora aliquando ovato-cuneata, nonnunquam ad 11.5 cm. longa, 3.5 cm. lata, lobis acuminatis, raro fere crenata. *Pedunculi* glabri, graciles, basi foliosi. *Capitula* 1-11, circiter 6 mm. transverse lata. *Involucri phylla* 16-34, 2.8-4 mm. longa, 1.2-1.4 mm. lata, oblanceolata, subacuminata-acuminata, marginibus fimbriato-ciliatis. *Flores radii* 18-40, ligulis 5 mm. longis, 1.4 mm. latis, caeruleis. *Receptaculum* 3 mm. latum, 2 mm. altum, hemisphaericum, nullis punctis. *Achenia* 2.5 mm. longa, 1.8 mm. lata, compressa, fusca, alata; corpus oblongo-cuneatum, marginibus paulo elevatis et tuberculis in disco parvis; alae tam latae vel latiores quam corpus, tenuiter et inaequaliter pinnatisectae. Pappus dimidio brevior quam intra alas incisurae altitudo.

Ascending or procumbent glabrous stoloniferous perennials up to 34.5 cm. high, freely branching from the base. Leaves cauline usually up to 6 cm. long, including the slender petiole, coarsely pinnatifid to pinnatipartite; segments about 7, up to 9 mm. long, 4 mm. broad, cuneate, acute, often mucronate. Lower leaves sometimes ovate-cuneate in rough outline, and occasionally up to 11.5 cm. long and 3.5 cm. broad with acuminate lobes, rarely almost crenate. Peduncles glabrous slender, leafy proximally. *Capitula* 1-11, about 6 mm. diameter. *Involucral bracts* 16-34, 2.8-4 mm. long, 1.2-1.4 mm. broad, oblanceolate, sub-acute to acute, with torn-ciliate margins. *Ray florets* 18-40, the rays 5 mm. long, 1.4 mm. broad, bluish. *Receptacle* 3 mm. broad, 2 mm. high, hemispherical, not pitted. *Fruit* 2.5 mm. long, 1.8 mm. broad, flat, brown, winged; body oblong-cuneate with slightly raised margins and small tubercles on the central region; wings equal to or exceeding the breadth of the body, shallowly and irregularly dissected. Pappus not more than half the depth of the notch between the wings.

Habitat: In well-drained situations in open forest country.

Range: Northern Tablelands and slopes of N.S.W.

Specimens examined:

New South Wales: Mt. Lindsay, 4.1914, H. M. R. Rupp (NSW); Blue Hole, near Armidale, 28.4.1941, M. Cumpston (NSW); Blue Hole, "Rocky situations on steep slopes among boulders", Consett Davis (holotype NSW; paratypes BRI, MEL); Dangar's Falls, 23.3.1941, 4.1941, B. Bassinett (NSW, BRI, MEL); George's Creek, Macleay R., Eucalypt Forest, 1,000', 26.1.1941, Consett Davis (NSW, BRI).

Vegetatively this species is characterized by rather lax foliage, the whole plant being weak and straggling. Variation in the leaves is noted, but is not considerable. In young plants a few radical leaves are present, which, with the lower cauline ones, give the appearance of a basal rosette. This, however, is lost with increased growth and the erect habit gives place to the typical procumbent condition.

No significant variation was seen in the fruit, all of which were very broadly winged, with a distinct tuberculate body. No resemblance is seen in vegetative characters, but details of the fruit indicate a close affinity with *B. dissectifolia*, the main difference being the broader dissected wing and scattered tubercles.

11. BRACHYCOME WHITEI SP. NOV.

(Text-figs. 19, 29; Plate vi, map 8.)

Holotype: Bybera, between Inglewood and Milmerian, 5.9.1935, C. T. White, n. 10751 (BRI).

Paratypes: Eight l.c. (BRI), one l.c. (NSW), one l.c. (MEL).

Herba annua, ramosissima, adscendens, ad 15 cm. alta, mic. glanduloso-paucipubescens—plane septato-pilosissima. Folia radicalia et cauline, ovato-cuneata-ovato-elliptica, pinnatifida aut apicem versus acute denticulata. Folia radicalia, gracili petiolo non neglecto, ad 6.8 cm. longa, 1.6 cm. lata, foliis caulinis paulatim brevioribus. *Pedunculi* filiformes, nudi. *Capitula* 1–54, 5 mm. transverse lata. *Involucri phylla* circiter 20, 2.2–3.8 mm. longa, 0.8–1.2 mm. lata, oblanceolata, sub-acuminata-acuminata, mic. serrata, glabra aut septato-pilosa. *Flores radii*, circiter 50, ligulis 6 mm. longis, 1 mm. latis, purpureis. *Receptaculum* 2–3.5 mm. latum, 1.2–2.8 mm. altum, late conicum, vix punctum. *Achenia* 1.5 mm. longa, 1–1.2 mm. lata, obovata, fusca-nigra; corpore utroque tuberculatissimo compresso; ala comparate lata, tenuis, margine glandulosa. Pappus tribus partibus achaenio brevior.

Ascending many-stemmed annuals (?), up to 15 cm. high; microscopically and sparsely glandular-pubescent to conspicuously septate-hairy. Leaves radical and cauline, ovate-cuneate to ovate-elliptical, pinnatifid or acutely toothed distally. Radical leaves up to 6.8 cm. long, including the slender petiole, 1.6 cm. broad, the cauline leaves progressively shorter. *Peduncles* filiform, naked, sometimes scape-like. *Capitula* 1–54, 5 mm. diameter. *Involucral bracts* about 20, 2.2–3.8 mm. long, 0.8–1.2 mm. broad, oblanceolate, sub-acute to acute, microscopically serrulate, glabrous or septate-hairy. *Ray florets* about 50, the rays 6 mm. long, 1 mm. broad, purple. *Receptacle* 2–3.5 mm. broad, 1.2–2.8 mm. high, broadly conical, scarcely pitted. *Fruit* 1.5 mm. long, 1–1.2 mm. broad, obovate, dark brown to black; body flattened, each face bearing numerous confluent tubercles which give an inflated appearance; wing relatively broad, thin, marginally glandular. Pappus about one-quarter the length of the fruit.

Range: Northern Queensland, Cape River to New South Wales border.

Specimens examined:

Queensland: Cape River, ? Coll. (MEL); Milray Station, S. of Pentland, North Kennedy district, "in Eucalypt forest on sand. Tufted annual with ascending to erect stems. Leaves dull green above, paler beneath. Ray white, disc yellow", 20.10.1936, S. T. Blake (BRI); between Bowen Downs and Mueller's Range, Ch. Weld Birch (MEL); Yalleroi, Mitchell district, 4.1946, M. S. Clemens (BRI); near Adavale, "lavender", 28.8.1923, W. Macgillivray (BRI); Warrego district, Gilruth Plains, near Cunnamulla, "Small tufted herb in red sandy soil, fairly common. Ray florets purple, disc florets yellow", 17.9.1938, S. L. Everist, n. 1638 (BRI); Bybera, "herb on sandy soil", 3.9.1934, C. T. White (BRI); Bybera, 5.9.1935, C. T. White, n. 10751 (BRI, holotype and 8 paratypes; paratypes NSW; MEL); Vict. Exped., 29.6.1861 (MEL).

The fruits of this species are remarkable in the presence of an inflated portion on each face, apparently formed by confluent tubercles, the curled hairs of which still persist. The possession of a thin wing and relatively conspicuous pappus indicates an affinity with *B. debilis*, a view which is supported by the close vegetative similarity between these two species. Since *B. debilis* is confined almost exclusively to Victoria and South Australia, it is not unlikely that these two species originated as subspecies, in one the curled glandular hairs being retained, while in the other they gave place almost entirely to tubercles which became confluent.

Although the series available is small, it consists of specimens from a relatively large area, so that a certain amount of vegetative variation is to be expected. The majority of the specimens examined have several rather weak branching stems, but those from Yalleroi bear a basal cluster of ovate-elliptical, almost crenate leaves, from which arise the slender scape-like peduncles.

In the Bybera specimens the sparse glandular hairs are microscopic, and an occasional septate hair is found, whereas in those from the Warrego district, the stems are macroscopically woolly, particularly at the leaf-stem axils. In the absence of ecological notes these variations are merely recorded without comment.

An interesting variation is noted in the fruits of the Adavale specimens, the wings of which are thrown into transverse folds, but are otherwise identical with those of the rest of the series. A specimen collected by the Victorian Expedition bears no locality data, but probably was collected from near the Loddon River, south-western New South Wales, and if so, is interesting from the point of view of distribution. However, it is a flowering specimen, and the fruit on which the diagnosis was made

Text-figures 19-22, 35, 36. Habit studies. $\times \frac{1}{2}$.

19. *B. Whitei* (Holotype). 20. *B. radicans* (Lectotype). 21. *B. lineariloba*. 22. *B. campylocarpa*. 35. *B. basaltica* var. *basaltica* (Lectoparatype). 36. *B. basaltica* var. *gracilis* (Lectotype).

are enclosed in an envelope accompanying the specimen. The possibility of these fruit having come from some other specimen cannot be overlooked. Owing to the uncertainty of the locality, and the absence of fruit from the plant itself, this species has not been recorded from New South Wales, though it may well occur there. The species is named after the collector, Mr. C. T. White, Government Botanist of Queensland.

12. *BRACHYCOME RADICANS* Steetz ex Lehmann, Pl. Preiss, 1 (1845), 429.
(Text-figs. 20, 30; Plate vi, map 9.)

Lectotype: Tasmania, Gunn, n. 513 (MEL).

Glabrous ascending stoloniferous perennials up to 30 cm. high. Leaves cauline, up to 15 cm. long, 6 mm. broad, linear to broad-linear, entire or with 1-4 linear lobes, occasionally oblanceolate, up to 8 mm. broad, obtuse, entire or irregularly and acutely toothed. *Peduncles* 1-2, leafy proximally, sometimes with a single bract immediately below the inflorescence. *Capitula* 8-10 mm. diameter. *Involucral bracts* about 18, up to 4.5 mm. long, 2.2 mm. broad, obovate, obtuse, torn-ciliate. *Ray florets* about 34, the rays 6 mm. long, 1.7 mm. broad, white or mauve. *Receptacle* 1.5 mm. broad, 2 mm. high, steeply conical, moderately pitted. *Fruit* 2 mm. long, 0.8 mm. broad, brown, oblong-cuneate, flattened; body bearing 2, or sometimes 3 longitudinal folds; wing inflated. Pappus conspicuous.

Habitat: Swampy ground.

Range: Tablelands of New South Wales, through highlands of Victoria and Tasmania.

Specimens examined:

New South Wales: Elderberry Crk., near Guyra, "edge of swamp, rays white", 24.2.1941, G. L. Davis (NSW); 10 miles S.E. of Guyra, "Swampy ground, rays pinkish-mauve", 18.2.1941, G. L. Davis (NSW, BRI); *Bullock Crk., New England, 2.1.1941, Consett Davis (NSW); Guy Fawkes Creek, near Ebor, "Swampy grassland", 24.1.1941, Consett Davis (NSW); Gudgenby, Queanbeyan, 14.1.1912, R. H. Cabbage (NSW); *Mt. Kosciusko, 12.1924, T. Harris (NSW).

Victoria: Omeo Morass, 12.1854, F. Mueller (MEL); Morass Creek, 15 miles N.E. of Omeo, 1.1922, H. B. Williamson (MEL); Morass Creek, near "The Brothers", 3,000', swamps, 31.1.1946, J. H. Willis (MEL); *Wannow R., D. McLachlan (MEL).

Tasmania: *South Esk R., Fenten's Ford, 9.12.1844, Gunn, n. 397 (NSW); *South Esk R., "Swamps", 12.1848 (?), C. Stuart, n. 403 (MEL); *Banks of South Esk R., near Perth, 12.1848, C. Stuart (MEL); South Esk R., between 1st and 2nd Basin, 1853, Gunn, n. 397 (NSW); *Arthur's Lakes, 18.2.1843, Gunn, n. 513 (NSW); Tasmania, 1844, Gunn, n. 513 (lectotype MEL; lectoparatype NSW); Tasmania, W. H. Archer (NSW); *Tasmania, Leibold (MEL).

The specimen selected as lectotype was acquired by the National Herbarium, Melbourne, from the Steetz collection, and the sheet to which it is affixed bears the inscription "*Brachycome radicans nobis*" in Steetz's handwriting. Since the data on the label accompanying the specimen agree with those quoted in the original description, there is no doubt that this is an authentic syntype specimen.

This species, like *B. dissectifolia*, is remarkable in the leaf-variation shown by an individual plant, all the leaves being rarely of the same type. A common condition in *B. radicans* is for the majority of the leaves to be entire, while one or two bear long irregularly placed lobes.

Variation in the fruit is slight, and confined to the degree of development of the longitudinal folds. The wings are unusual in their inflated nature, and for this reason they resemble a margin, except for the fact that the body of the fruit is a distinct and separate structure. Among existing species *B. radicans* shows a closer affinity with *B. dissectifolia* than with any other, the main distinction, so far as the fruit is concerned, being the expression of a new line of development, the inflation of the wing.

13. *BRACHYCOME LINEARILoba* (DC) Druce.
Rep. Bot. Exch. Cl. Brit. Isles, iv (1917), 610.
(Text-figs. 21, 31; Plates vi, map 10; viii, 1.)

Synonymy: *Steiroglossa lineariloba* DC., Prod. vi (1838), 39. *Brachycome pachyptera* Turez., Bull. Soc. Mosc., xxiv (1851), 175.

Lectotype: Wet plains, Lachlan R., 29.7.1817, A. Cunningham (GENEVA).

Lectoparatype: Molle's Plains, Lachlan R., interior of N.S.W., 10.7.1817, A. Cunningham (GENEVA).

An apparently stemless (?) annual up to 21 cm. high, glabrous distally, with a few long septate hairs proximally. Leaves usually forming a basal rosette, up to 8.3 cm. long, pinnatisect with 6-9 segments up to 1.3 cm. long, 1 mm. broad, obtuse, occasionally with a short filiform proximal lobe. *Scapes* glabrous, naked. *Capitula* 1-70, up to 7 mm. diameter. *Involucral bracts* 10-16, 3.5-4 mm. long, 3-4 mm. broad, entire to slightly torn-ciliate, broadly obovate, obtuse, frequently purple at the margins. *Ray florets* 10-16, the rays 1-1-7 mm. long, 0.5-1.5 mm. broad. *Receptacle* 2.5 mm. broad, 1.5-2 mm. high, hemispherical, moderately to deeply pitted. *Fruit* 3.2-4.5 mm. long, 1.6-2.5 mm. broad, broad-cuneate in outline. Body terete, demarked by a groove from the turgid wings which bear long silky glandular hairs laterally. Pappus conspicuous, the bristles of unequal length and fused in bundles.

Range: Western districts of New South Wales and Victoria, south-eastern South Australia northward to Warrina. Apparently rare in Western Australia.

Specimens examined:

New South Wales: *Govt. N.W. Exped., 1903, H. Basedow (NSW); Lauradale to Bourke, 4.10.1912 (NSW); Darling R., near Bourke, 1886, A. Wurfel (MEL, NSW); Waroo, via Bourke, 10.1938, K. I. Morris (BRI); Upper Darling R., 1886, B. Kennedy (MEL); Caiwarro, near Darling R., 1886, J. Cotter (MEL); Darling R., F. Mueller (MEL); Cobar, 8.1911, L. Abrahams (NSW); Nyngan, 8.1903, J. L. Boorman (NSW); Wilcannia, 20.8.1935, J. W. Vickery and I. M. Pidgeon (NSW); Torrowangee, gibber plains, red loam, 10.1940, N. C. W. Beadle (NSW); Broken Hill and Torrowangee, 8.1893, H. Deane (NSW); Broken Hill, 7.1920, A. Morris (NSW); Broken Hill, 8.1926, E. Cheel (NSW); Stephen's Creek, Broken Hill, 12.8.1928, A. Morris (BRI); Menindie, river flat, 9.1946, N. C. W. Beadle (NSW); Lachlan R., 9.1878, F. Mueller (MEL); *Condobolin flats, 8.1897, J. H. Maiden (NSW); Wooyes Palestine, near Condobolin, 1896, Clements (NSW); *25 miles S.E. of Condobolin, heavy self-mulching grey-brown clay loam, under Savannah Woodland of *E. populifolia*, 5.1943, N. C. W. Beadle (N.S.W.); *Til Til, "salt-bush plain, grey clay loam", 8.1942, N. C. W. Beadle (NSW); Wyalong, 3.9.1915, J. W. Dwyer (NSW); Hay, 22.9.1889, J. J. Fletcher (NSW), Zara, near Hay, 2.1904, E. Officer (NSW); Jerilderie, 10.1920, Dwyer (NSW); R. Darling, 28.10.1860, Vict. Expl. Exped. (MEL).

Victoria: Murray desert, ?F. Mueller (MEL); Murray R., ?F. Mueller (MEL); Mallee, 10.1898, C. French (MEL); Swan Hill, Gummon (MEL); Kerang, 1887, J. Minchin (MEL); L. Albacutya, Mallee, 10.1899, C. Walter (NSW); Wimmera, 1884, Johnstone (MEL); Wimmera, 10.1900, C. Walter (NSW); Alston's Rd., S. Wycheproof, 23.9.1918, W. W. Watts (NSW); Boort, 1894, A. Purdie (MEL); Donald, Curdie (MEL); Dimboola Shire, 7.8.1898, 21.8.1892, F. M. Reader (MEL); Lubeck, 11.1903, McLennan (NSW); Talbot, 6.12.1883, F. Mueller (MEL).

South Australia: Warrina, M. Koch (AD); between Stokes Range and Cooper's Crk., Wheeler (MEL); Arcoona West of L. Torrens, 8.1927, B. J. Murray (AD); Mt. Lyndhurst, 8.1898, M. Koch (MEL, BRI, AD); Mt. Lyndhurst, 2.8.1920, H. W. A. (JMB); *Beltana, 17.8.21, J. B. Cleland (JBC); Mt. Parry, Flinder's Ra., 8.1883, R. Tate (AD, JMB); Ediowie, 10.1897 (NSW); Wilpena pound, 17.11.1918, J. M. Black (JMB); Wilpena pound, 30.11.1930, J. B. Cleland (JBC); Hawker, 8.1883, R. Tate (AD); Hawker, "Violet", 3.10.1916, J. M. Black (JMB); Hawker, 3.9.1941, J. B. Cleland (JBC); Hawker to Orroroo, 24.9.1936, G. B. Clarke (AD); Alderman's Paddock, Koonamore, 24.8.1930 (AD); Southern Cross Tank, Koonamore, 19.8.1930 (AD); Quorn, 27.8.1936, 2.9.1941, J. B. Cleland (JBC); Carricton, 29.9.1916, J. M. Black (JMB); Flinder's Ra., near Pt. Augusta, "White", 13.10.1937, J. B. Cleland (JBC); Pt. Augusta west, "Rays white to light violet", 29.9.1920, J. M. Black (JMB); Pt. Augusta, 9.1.1941, J. B. Cleland (JBC); Melrose, 15.10.1915, J. M. Black (JMB); *Pt. Pirie, 15.8.1939, J. B. Cleland (JBC); near Gladstone, 19.9.1906, 9.10.1916, J. M. Black (JMB); Lincoln Gap, 24.9.1942, J. B. Cleland (JBC), "At streams in front of the Burra Mine", 10.1851, F. Mueller (MEL); Deep Crk., 5 miles S.E. of Burra, 24.8.1946, J. B. Cleland (JBC); Emu Downs, 23.9.1942, J. B. Cleland (JBC); Renmark, 10.1915, J. M. Black (JMB); Lyrup, R. Murray, 8.1922, H.W.A. (JMB); Pungonda, 5.10.1915, J. M. Black (JMB); Berri, 1924, C.D.A. (JMB); *Blanchetown, 8.1881, R. Tate (AD); Blanchetown, 1.10.1915, J. M. Black (JMB); Halbury, 6.9.1909, J. M. Black (JMB); Pt. Pearce, 15.8.1937, J. B. Cleland (JBC, JMB); Sedan, 9.1884, O. Tepper (MEL); near St. Vincent's Gulf, 9.1884, O. Tepper (MEL); Dry Creek, 17.8.1880, R. Tate (AD); *Marino, 8.1879, R. Tate (AD); Hallett's Cove, 26.8.1906, H. H. W. Griffiths (JMB); Hallett's Cove, 9.10.1920, J. B. Cleland (JBC); Mannum, 30.9.1915, J. M. Black (JMB); Monarto South, 28.8.1919, E. H. Ising (JMB); Monarto South, 25.9.1920, J. B. Cleland (JBC); Kinchina, 1.8.1925, 9.1927, J. B. Cleland (JBC, JMB); across R. Murray, 10.10.1848, F. Mueller (MEL); Karoonda, 18.8.1924, J. B. Cleland (JBC); Mulgundaire, near L. Alexandrina, 3.10.1906, J. M. Black (JMB); Murray Scrub, 1.9.1897, O. E. Menzel (AD); Pinnaroo, 12.10.1918, J. M. Black (JMB); *Pinnaroo, 8.1927, J. B. Cleland (JBC); Lincoln Gap, 24.9.1942,

J. B. Cleland (JBC); Caroon, Iron Knob, 25.8.1928, J. B. Cleland (JBC); 7 miles east of Iron Knob, 25.8.1928, J. B. Cleland (JBC); Yardea, 23.8.1928, J. B. Cleland (JBC, JMB); Minnipa, 9.1916, R. Tate (AD); Davenport Crk., Gawler Ra., 8.1928, J. B. Cleland (JMB); Talia, 20.8.1925, J. B. Cleland (JBC, JMB); *Mt. Wedge, 22.8.1925, J. B. Cleland (JBC); Tooligie, 14.8.1928, Cummins (JMB, JBC); Port Lincoln, 10.10.1909, H. H. W. Griffiths (JMB); Koonibba, 20.8.1928, J. B. Cleland (JBC); Cape Thivenard, J. M. Black (JMB); Fowler's Bay, 1879, R. Tate (AD); Fowler's Bay, 10.1907, T. Brown (NSW); Ooldea Soak, 17.8.1939, J. B. Cleland (JBC).

Western Australia: "W.A., No. 205", J. Drummond (haptotype of *B. pachyptera*, MEL); Lakeside, 8.98, W. V. Fitzgerald (NSW).

A specimen collected by J. Drummond bearing the type citation of *B. pachyptera* ("W.A., No. 205") is in the National Herbarium, Melbourne. This specimen has been used as a basis of comparison, but as it is unknown whether it is an authentic syntype, it has been nominated haptotype. Syntype material of *Steiroglossa lineariloba* is in De Candolle's herbarium at Geneva, and consists of two specimens apparently collected by A. Cunningham, and bearing the labels "29 July, 1817, wet plains, Lachlan R.", and "10 July, 1817, Molle's Plains, Lachlan R. Interior of N.S.W.", respectively. A photograph of these specimens shows them to resemble *B. pachyptera* very strongly, and examination of a floret and young fruit from the latter specimen confirms this resemblance. *B. lineariloba* was described under the generic name of *Steiroglossa* in 1838, and hence the specific epithet takes priority over that of Turczaninow. De Candolle's two specimens were nominated lectotype and lectoparatype of *S. lineariloba* and also of the specific name in its new combination.

Variation in size within this species is considerable, fruiting plants only 2 cm. high having been examined. In these dwarf plants, which are by no means uncommon, the leaves are frequently entire. This is taken to indicate a short growing period, and the consequent persistence of the first leaves which, in larger plants with a longer growing period, are replaced by the characteristic pinnatisect type of foliage. There is little or no difference in the size of the mature fruit in dwarf and large plants.

Variation in size of the rays is discontinuous and apparently two natural populations are in existence, one of which constantly bears rays about 1.1 mm. long, while the other bears them 6-7 mm. long. As a large proportion of the specimens examined are in fruit, and attempts to link up the size of the ray with some other character have failed, there is no way of determining to which population a particular fruiting specimen belongs. It is not considered desirable to erect a new variety until further specimens are forthcoming.

The position of *B. lineariloba* in any scheme attempting a natural grouping of species is a difficult one, and depends entirely on the interpretation of the swollen tissue on either side of the body of the fruit. If this tissue is considered to be a margin, this species should be grouped elsewhere, but if it is taken as being morphologically a greatly inflated wing, then it is simply the expression of a tendency already apparent in *B. radicans*.

14. BRACHYCOME GRAMINEA (Labill.) F. Muell., Frag. Phytog., 1 (1858), 49.

(Text-fig. 32; Plate vi, map 11.)

Synonymy: *Bellis graminea* Labill., Pl. Nov. Holl., ii (1806), 54. *Paquerina graminea* Cass. in DC., Prod. v (1836), 306.

Lectotype: "Bellis graminea", Tab. 204, Pl. Nov. Holl., ii (1806).

More or less branching, weakly erect or ascending herbs up to 70 cm. high, perennating by means of stolons. Branches, and sometimes young leaves, sparsely and minutely glandular-pubescent. Leaves cauline, frequently crowded towards the base of the stem, up to 14.5 cm. long, 7 mm. broad, narrow to moderately oblanceolate, rarely linear, entire, subacute to acute, tapering proximally, the midrib prominent below. *Capitula* 1-5, about 6 mm. diameter. *Peduncles* leafy proximally. *Involucral bracts* 18-20, up to 3.5 mm. long, 0.8-1.3 mm. broad, linear, obtuse to subacute, glandular on the outer surface, the margins minutely serrulate. *Ray florets* 20-34, the rays 9 mm. long, 2 mm. broad, apparently always blue or violet. *Receptacle* 1.6 mm. broad, 1 mm. high,

convex, deeply pitted. *Fruit* 2 mm. long, 1.6 mm. broad, obovate, flattened, turgid with a slight central depression and rounded margins. Pappus minute.

Habitat: Moist to marshy situations.

Range: Southern Queensland through tablelands of New South Wales, to Victoria and Tasmania, where it is widely distributed. In South Australia it is confined to the south-eastern region.

Specimens examined:

Queensland: *Southport, "sea coast", 12.1856, F. Mueller, n. 1421 (MEL); Dec.-Feb., 1855-56, F. Mueller (MEL).

New South Wales: *Moona Plains, 2.1899, A. R. Crawford (NSW); *Capertee, 11.1900, J. L. Boorman (NSW); *Newnes Junction, 4.1914, A. A. Hamilton (NSW); Blackheath, 4.1909, J. H. Maiden (NSW); *Blayney, 12.1907, J. L. Boorman (NSW); Yarrangobilly Caves, 2.1897, E. Betche (NSW); Nimitybelle to Cooma, 12.1896, J. H. Maiden (NSW); Nimitybelle, 2.1893, E. Betche (NSW); *Delegate, 1.1910, W. Forsyth (NSW).

Victoria: *Lower Mitta Mitta R., 1.1874, F. Mueller (MEL); Bogong high plains, 1.1923, H. B. Williamson (MEL); *Banks of Morass Crk., at "the Brothers", near Benambra, about 3,000', 31.1.1946, J. H. Willis (MEL); Omeo, "on grassy places near lagoon", 12.54 (MEL); Omeo, Morass, F. Mueller (MEL); Lake Victoria, 28.4.1848, F. Mueller (MEL); *Inornton, 15.4.1911, P. R. H. St. John (MEL); *Yarra R., "among Juncaceae", 23.1.1853, S. C. Hannaford (MEL, NSW); *Port Phillip (BRI); Little R., Fullager (MEL, NSW); *Lorne, H. B. Williamson (MEL); *Pyrenees, "moist places", E. Wilhelmi (MEL); *Fiery Creek, W. H. Whan (MEL); *Hall's Creek, F. Mueller (MEL).

South Australia: Lyrup, 8.1922, J. M. Black (JMB); *Mannum, 5.3.1883, R. Tate (AD); Swanport, Storey (MEL); R. Murray, Miller (JMB); Robe, 4.1912, Miller (JMB); Robe, 5.3.1941, J. B. Cleland (JMB, JBC); Cape Banks, 27.2.1945, J. B. Cleland (JBC); Mt. Gambier, 27.5.1925, J. B. Cleland (JBC).

Tasmania: Mouth of George's R., George's Bay, 12.1877 (MEL); *George's Bay, 6.1892 (NSW); George's Bay, W. V. Fitzgerald (NSW); George's Bay, A. Simson (BRI); Ronald Neck, Marsh, 11.1.1837, Gunn, n. 834 (NSW); "neck", 27.2.1837, Gunn (NSW); Freycinet's Penin., 4.1906, L. Rodway (HO); Freycinet's Penin., "muddy plains", 1.1899, L. Rodway (HO); *Bridgewater, 1.1930, C. E. Lord (HO); *between Bridgewater and New Norfolk, "marshy ground", 21.2.1869 (MEL); Eaglehawk Neck, "cranny in cliff above sea beach", 16.5.1939, H. D. Gordon (HO); Port Arthur, 1892, J. Bufton (MEL); Boomer, near Dunally, "margin of Salt Marsh", 13.1.1944, W. M. Curtis (HO); *Risdon, 4.1894, 12.1906, L. Rodway (HO); *Cole's Bay, 20.4.1930, L. Rodway (HO); *Macquarie Hb., "margin of estuary", 30.12.1846, W. W. Watts, n. 812 (MEL); Settlement Is., Macquarie Hb., 1842, J. Milligan (MEL); *Tas., W. H. Archer (NSW); *Van Diemen's Land, R. Brown (MEL).

This species was originally described under the genus of *Bellis* but later became the genotype of *Paquerina* H. Cass (DC., Prod. v, 1836, 306), in which genus it remained until it was incorporated in *Brachycome* Cass by Mueller (Frag. i, 1858, 49).

Although no doubt exists as to the identity of *B. graminea* considerable confusion has arisen with regard to type selection. The author is indebted to Professor H. Humbert, Director of the National History Museum, Paris, for the following information concerning allegedly syntype material of *Bellis graminea* presented to that institution by M. Webb: "Feuilles d'herbier de *Bellis graminea* comprenant 7 pieds portant 5 capitules, en fleur semble-t-il." Photographs of these specimens show that the leaves are pinnatisect, with 3-7 lobes, and the general appearance is of robust and somewhat woody plants, which consequently do not agree with Labillardière's original description or the accompanying figure. The opinion formed from the photographs that these specimens are not conspecific with *Brachycome graminea* (Labill.) F. Muell., is supported by examination of florets from two specimens ("Austral. Felix, Ferd, Mueller, 1863", and "Port Phillip, C. Walter") sent by Professor Humbert with the following comment: "Je vous envoie donc quelques capitules prélevés sur des échantillons moins rares et paraissant identiques à ceux de Labillardière." The fact that the anther connectives bear no terminal appendages is conclusive evidence that they do not belong to specimens of *B. graminea*. It is suggested that some confusion of Labillardière's original labels occurred and that the specimens in Paris now bearing the identification *B. graminea* are in effect *B. ciliaris*, which was also collected by him in Australia. Having failed to trace further specimens of this species collected by Labillardière, it was considered that they were no longer extant and the recommendation put forward in the International Rules of Botanical Nomenclature to cover such an emergency was adopted (Section 2, Art. 18: "the name of . . . a species or group of lower rank is usually a specimen or preparation. In some

species, however, the type is a description given by a previous author"). Labillardière's excellent figure in *Pl. Nov. Holl. ii* (1806), t. 204, was accordingly selected as lectotype, and a specimen in the National Herbarium, Melbourne, collected by Robert Brown in Tasmania, which agrees exactly with this figure, was used as a basis of comparison for all specimens. It is unfortunate that this latter specimen bears no fruit, but accompanying the lectotype is an enlarged drawing of a fruit which, with the original description, leaves no doubt as to their nature.

The three varieties of *Paquerina* described by Sonder (*Linnaea*, xxv (1852), 478) have never been adopted in general terminology and were not legitimately transferred to *Brachycome* by Mueller. Authentic syntype material of var. *angustissima* and var. *heterophylla* has been located at the Gray Herbarium, Harvard, and of the latter variety only, at the National Herbarium, Melbourne. The author is indebted to Dr. Bernice G. Schubert for photographs of the Harvard specimens which, supported by examination of fruit and florets loaned for that purpose, show that both these so-called varieties have been misidentified and are really typical specimens of *B. parvula* Hook f. Type selection has been made in each case (var. *heterophylla* Sond., Mt. Sturgeon, F. Mueller, lectotype, MEL; lectoparatype, HARVARD; var. *angustissima* Sond., Yarra, F. Mueller, lectotype, HARVARD), but the varieties as such are abandoned. Efforts to trace specimens of var. *latifolia* Sond. have not been successful so the original description is merely quoted: "folia elongata 3-4 pollicaria, lamina bipollicari 4-5 lin. lata". It is probable that this variety was also based on specimens of *B. parvula*.

Owing to the similarity between certain members of *B. graminea* and *B. angustifolia* it is not always possible to distinguish them in the absence of reasonably mature fruit. A number of flowering specimens are listed (with a distinguishing mark) which have been carefully compared with authentic specimens, but it is possible that in one or two cases a misidentification may have occurred.

In the absence of collector's notes with regard to habitat, the variation noted can merely be recorded with the comment that it is probably correlated with the situation in which the particular specimens were growing. Typically the plants are weak and unable to support their own weight, which suggests growth amongst tall grass or other supporting plants. Such specimens normally bear relatively few and long leaves, the longest recorded being 14.5 cm. Many other specimens have been examined in which the growth is tufted, and the individual plants considerably smaller. In these instances there is a relative increase in the number of leaves which are mainly clustered towards the base of the stem giving the appearance of radical leaves. These plants have not the lax appearance of the larger specimens and are probably growing among short herbage. Intermediate types of growth have also been noted and the two extremes occur over the whole range, and are not sufficiently marked to justify their inclusion in separate categories.

The position of *B. graminea* in a natural arrangement of species is a controversial matter, and hitherto it has been considered to bear wingless fruit. Dissection of the fruit, however, shows a central body completely enclosed in softer tissue of the same spongy consistency as the inflated wing of *B. lineariloba*. This, in the present author's opinion, suggests its origin from an ancestor bearing inflated wings, the inflation of which proceeded until the wing from each side of the fruit converged in the midline, thereby completely enclosing the body. Apart from this no other origin suggests itself, and no affinity has been found between *B. graminea* and any species of the truly wingless groups.

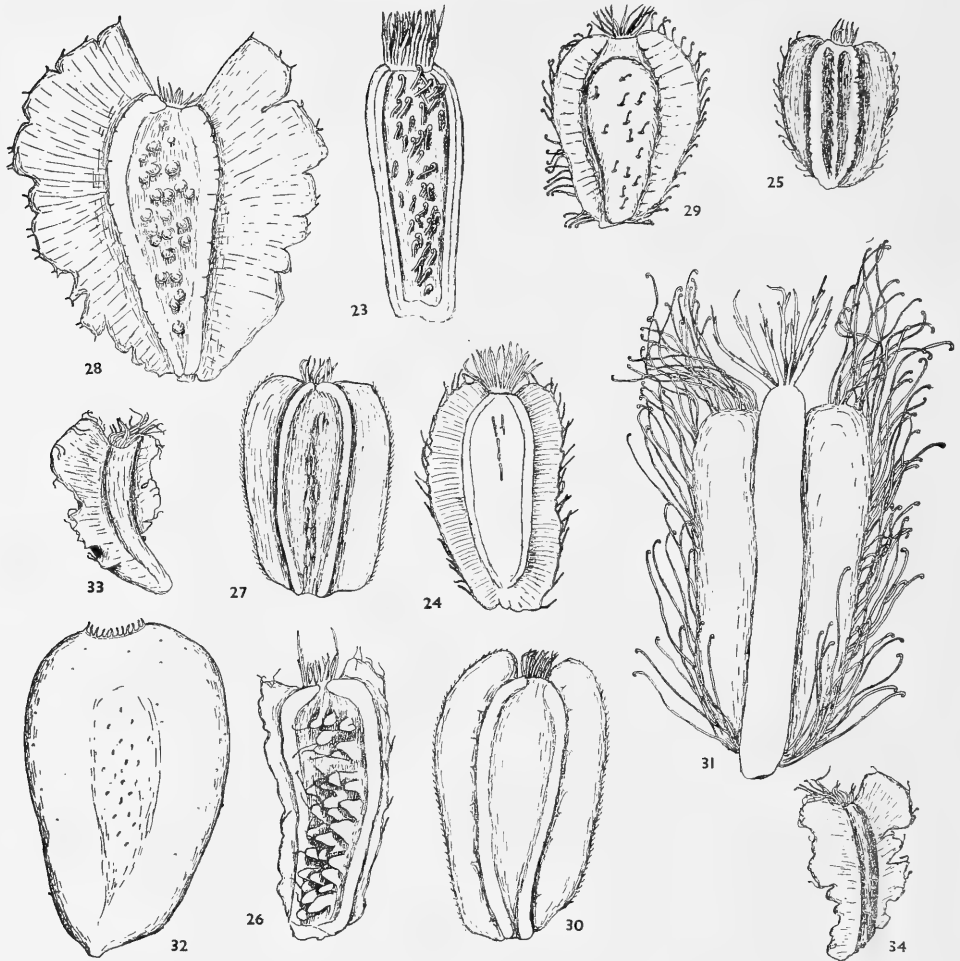
15. BRACHYCOME CAMPYLOCARPA J. M. Black.

Proc. Roy. Soc. S.A., lli (1928), 228.

(Text-figs. 22, 33, 34; Plate vi, map 12.)

Lectotype: Minnie Downs, Diamantina River, "Flooded plains, 6-9 in. high", 8.1926, L. Reece (JMB).

Lectoparatype: l.c. (MEL).

Text-figures 23-34. Fruit. $\times 17$ approx.

23, *B. leptocarpa*. 24, *B. debilis*. 25, *B. ptychocarpa*. 26, *B. angustifolia*.
 27, *B. dissectifolia*. 28, *B. procumbens*. 29, *B. Whitei*. 30, *B. radicans*.
 31, *B. lineariloba*. 32, *B. graminea*. 33, *B. campylocarpa*. Inner side of
 fruit. 34, *B. campylocarpa*. Outer side of fruit.

Many-stemmed erect or ascending annuals (?) up to 28.5 cm. high, septate-hairy at leaf-stem axils, otherwise glabrous. Leaves radical and cauline, up to 11.2 cm. long, singly or doubly pinnatisect with sheathing bases; radical leaves rarely entire. Leaf-segments 3-5, up to 2 cm. long, 2 mm. broad, sub-acute to obtuse. *Peduncles* glabrous, proximally leafy. *Capitula* up to 21, 7-9 mm. diameter. *Involucral bracts*, 14-16, 3.5-5 mm. long, 2.2-2.8 mm. broad, obovate to broad-elliptical, glabrous, entire, the outer ones obtuse. *Ray florets* 12-23, the rays up to 1 cm. long, 2.5 mm. broad. *Receptacle* up to 6 mm. broad, 3 mm. high, conical to hemispherical, not pitted. *Fruit* 2-2.7 mm. long, 1.2 mm. broad, black, oblong-cuneate, strongly curved; body terete; wings thick and distally expanded with long marginal glandular hairs. Pappus large and conspicuous.

Range: Apart from two records in the Scone district, this species is confined to south-western and southern Queensland, western New South Wales and northern South Australia.

Specimens examined:

Queensland: Birdsville, "at edge of flood plain at foot of sandhill. Bushy full-green annual, to 6 in.", 19.7.1936, S. T. Blake (BRI); Yelarbon, 9.1919, C. T. White (BRI).

New South Wales: Cuttabri, Pilliga Scrub, 8.1913, J. L. Boorman (NSW); Louth, "river flat, grey silt loam", 4.1941, N. C. W. Beadle (NSW); Curlewis, 8.1913, E. Breakwell (NSW); *Scone, 8.1913, E. Breakwell (NSW); Lachlan R., 9.1878, F. Mueller (MEL); 10 miles E. of Mossgiel, "grey silt loam on saltbush plain", 8.1942, N. C. W. Beadle (NSW, BRI); Poplita, 19.9.1925, A. Morris (NSW); R. Darling, Victor. Exped. (MEL).

South Australia: Minnie Downs, Diamantina R., 8.1926, L. Reece (lectotype JMB, lectoparatype MEL); Diamantina R., 1931, L. Reece (JMB); 20 miles w. of Oodnadatta, 5.8.1933, J. B. Cleland (JBC); Mt. Lyndhurst, 8.1898, M. Koch (AD, NSW).

This species has hitherto been known only from three specimens from the Diamantina district, all in an unsatisfactory state of preservation. It is now shown to have a relatively wide range, and while by no means common, is far from rare in the western districts of New South Wales. The reason these other specimens have been for so long unrecognized, is the strong superficial similarity to *B. lineariloba*, with which species they were invariably included. These two species, although apparently closely related, can be readily separated at any stage. In habit, *B. campylocarpa* is distinct in its many branched stems and cauline leaves, characters never shown by *B. linearifolia*. The extreme and characteristic curving of the fruit is seen at an early stage, as is also the distal expansion of the wing, which results in each fruit partially overlapping an inner one, so that they are all tightly packed on the head. A conspicuous feature of the young fruit is the long marginal glandular hairs. These, in *B. campylocarpa*, decrease in number as development proceeds, until at maturity they are relatively few, along the edges of the wing. The syntype specimens all bear fruit at an advanced stage of maturity, and are a dull black in colour, whereas those of other specimens examined, being presumably not quite mature, are brown. The inflation of the wings is a character indicating affinity with *B. lineariloba*, though in this case it is particularly apparent distally. When full maturity is reached the wing becomes margin-like and brittle, though throughout development the body is a distinct structure. These two species are also separable on details of the pappus, the bristles of which are silky-white, of irregular length and grouped in bundles in *B. lineariloba*, while in *B. campylocarpa* they are usually very light brown, and of equal length joined, if at all, only at the base. This last feature is of use in identifying specimens bearing only very young fruit. A definite affinity exists between these two species which is particularly marked in fruits of *B. campylocarpa* which are not quite mature. It is apparent that they belong to the same line of development, and if not actually closely related at least are expressions of similar evolutionary trends.

3. Superspecies BASALTICA.

16. BRACHYCOME BASALTICA F. Muell.

Fragmenta phytographica, i (1858), 50.

Branching glabrous perennials up to 62.5 cm. high. Leaves radical and cauline or only cauline, up to 9.5 cm. long, broad- to ovate-lanceolate or linear and grass-like, sessile, entire, sub-acute to acute. *Peduncles* more or less leafy proximally. *Inflorescences* 5-8 mm. diameter, 1-3 present. *Involucral bracts* 19-30, 2.5-3.6 mm. long, 0.9-1.5 mm. broad, narrow-oblong to obovate, glabrous, entire, obtuse to acute. *Ray florets* 20-50, the rays 3.5-8 mm. long, 1.1-2.5 mm. broad, white. *Receptacle* 2-2.3 mm. broad, 1.6-2 mm. high, broadly convex, moderately pitted. *Fruit* 1.4-2 mm. long, 0.7-1 mm. broad, light to dark brown, narrow-cuneate to obovate, flattened at first, becoming more or less turgid at maturity, conspicuously tuberculate on each face, with smooth margins which tend to become obscured in very turgid fruit. Pappus a minute rim, which may be irregularly broken into numerous blunt finger-like processes.

Key to the varieties.

Leaves broad- to ovate-lanceolate, lower ones 3-veined below var. *α basaltica*.
 Leaves narrow lanceolate to linear, grass-like, 1-veined below var. *β gracilis*.

Brachycome basaltica F. Muell., var. *α basaltica* comb. et stat. nov.

(Text-figs. 35, 42; Plate vi, map 13.)

Lectotype: Peak Downs, Brisbane River, 12.1856, F. Mueller (MEL).

Lectoparatypes: Five. Peak Downs, Brisbane River, 12.1856, F. Mueller (MEL).

Usually robust, up to 47 cm. high, with cauline, stem-clasping leaves. Lower leaves prominently 3-veined below, sub-acute, broad- to ovate-lanceolate, 3.2-5.5 cm. long, 0.6-1.4 cm. broad. Upper leaves smaller, acute, narrow-lanceolate. *Involucral bracts* 23-30, narrow-oblong, acute.

Habitat: No data available.

Range: Queensland, Peak Downs to New South Wales border.

Specimens examined:

Peak Downs, 12.1856, F. Mueller (MEL, lectotype, lectoparatypes); *Gordon Downs, H. Weld Blundell (BRI); Keppel Bay, F. Mueller (MEL); Wide Bay, L. Leichhardt (MEL); Ipswich, 12.1908, T. F. Hall (BRI); Boonah, 6.11.1935, N. Michael (BRI); Rosewood Station, F. M. Bailey (BRI); Gatton College, 10.1906, J. F. Bailey (BRI); Cunningham Gap, Mts. (BRI, MEL).

The Syntype series consists of six specimens from which a lectotype was selected, and the remainder nominated lectoparatypes. The caption on the label accompanying these specimens reads "Peak Downs. Brisbane River", but as these are two distinct localities, it is taken that the preposition "to" is implied between them. Mueller does not quote any specific specimen in the original description, recording merely "on basalt plains from Peak Range district to Darling Downs".

No significant vegetative variation has been noted within the very restricted range of this variety. In general the lowest leaves are relatively small and ovate, passing suddenly into the typical lower cauline leaves, but this is a character to be correlated with the age of the plant.

Brachycome basaltica F. Muell., var. *β gracilis* Benth.

Fl. Aust. iii (1866), 515.

(Text-fig. 36; Plate vi, map 13.)

Lectotype: Keppel Bay, Thozet (MEL).

Lectoparatypes: Twelve, Keppel Bay, Thozet (MEL).

Slender and weakly erect, up to 62.5 cm. high, with grass-like leaves. Radical and lower cauline leaves narrow-lanceolate to linear, up to 9.5 cm. long, 2.5 mm. broad, the uppermost leaves almost filiform. *Involucral bracts* 19-21, obovate to narrow-oblong.

Ray florets 40-50.

Habitat: Swampy ground.

Range: Southern coast of Queensland, through western New South Wales to Central Victoria, and Murray lands of South Australia.

Specimens examined:

Queensland: Keppel Bay, Thozet (MEL, lectotype, lectoparatypes); *Head Station, Wide Bay, "swamp", 3.8.1843, L. Leichhardt (MEL).

New South Wales: Boggabri, 7.11.1909, R. H. Cambage (NSW); Bogan R., 2.1846, T. L. Mitchell (MEL); Co. Cadell, "red gum forest", spring, 1941, N. C. W. Beadle (NSW).

Victoria: Benjeroop, 11.1896, C. Walter (MEL); Boorhaman, 12.1925, H. B. Williamson (MEL); Boorhaman, 9.10.1942, R. A. Black (RAB); Nathalia, 10.1930, J. H. Willis (MEL); 3 miles e. of Nagambie, "swamp", 9.1942, Consett Davis (MEL, NSW).

South Australia: The Narrows, Nonning, 11.7.1945, J. B. Cleland (JBC); Kingston-on-Murray, 12.2.1942, J. B. Cleland (JBC); Mannum, 6.12.1936, C. M. Eardley (AD); Murray Bridge, "trailing plant in swamp", 30.12.1895 (AD); margin of Lake Alexandrina, 4.1848, F. Mueller (MEL).

The Syntype series of this variety in Australia includes a number of specimens from Keppel Bay in the National Herbarium, Melbourne, the labels of which are all marked as having been examined by Bentham, and in addition the sheets are enclosed in a folder on which is written "var. *gracilis*" in Bentham's script. From this series a lectotype and twelve lectoparatypes were selected. Bentham (1866) records this variety from three localities in New South Wales (Macquarie Marshes, Murray and Darling Rivers), but the only specimen from this State at present in any Australian herbarium is one from Boggabri in the National Herbarium, Sydney. It seems likely that var. *gracilis* previously occupied a more extensive range, having migrated to the coast of Queensland along the basin of the Darling, subsequently dying out over most of its range. Being a marsh plant with high-water requirements, it could not survive prolonged drought conditions. It is suggested that var. *basaltica* originated as an ecotype of var. *gracilis* in Queensland, occupying drier and better drained situations.

Variation is slight, confined to small differences in height and leaf measurements, which are never sufficient to alter the general appearance of the plant. This lack of variation indicates that the species itself has lost its genetic plasticity, and does much to confirm the suggestion that it is dying out.

When only upper leaves are represented on a specimen there is a superficial resemblance to *B. trachycarpa* F. Muell., but the two species are readily separated on details of the fruit and anthers. This similarity reflects no close phylogenetic relationship, and the two species are widely separated.

Whether the irregularly broken ring of tissue at the summit of the fruit actually represents a pappus or not is a question which can only be decided by detailed study of its development. In the author's opinion it is unlikely that this is so, but the structure observed is referred to as a pappus for the sake of convenience.

17. BRACHYCOME ASCENDENS SP. NOV.

(Text-figs. 37, 43; Plate vi, map 14.)

Holotype: Robert's plateau, National Park, Queensland, "Herb growing on rock faces in open forest. Flowers lavender", 28.5.1929, C. T. White, n. 6078 (BRI).

Paratypes: l.c., seven (BRI, NSW, MEL).

Herba perennis, ascendens, ramosa, ad 31 cm. alta, glanduloso et septato-pilosa. Folia caulina ad 2-3 cm. longa, cuneata, 2-8 acuminatis, cuneatis lobis aut dentata-pinnatifida. Folia radicalia herbis junioribus interdum adsunt. *Pedunculi* pilis glandulosis aut paucis septatis in apice pilosi, foliosi in basi. *Capitula* 1-8, transverse lata 9 mm. *Involucris phylla* 16-18, circiter 4.5 mm. longa, 1.6 mm. lata, oblanceolata, glabra aut minutissime glandulosa, acuminata, margine fimbriato-ciliata. *Flores radii*, circiter 20, ligulis 4 mm. longis, 1 mm. latis, violaceis. *Receptaculum* 2.5 mm. latum, 2.2 mm. altum, late conicum, punctis satis altis. *Achaenia* 2-2.2 mm. longa, 1.3 mm. lata, oblonga, compressa, fusca; corpus tuberculis in media partiparvis, margine alaesimili inaequaliter secta a laterale extentum. Pappus conspicuus.

Ascending branching perennials (?) up to 31 cm. high, glandular and septate-hairy. Leaves cauline, up to 2.3 cm. long, cuneate in rough outline, dentate to pinnatifid, with 2-8 acute cuneate lobes or teeth. Radical leaves may be present in young specimens. *Peduncles* glandular or sparsely septate-hairy distally, leafy proximally. *Capitula* 1-8, 9 mm. diameter. *Involucral bracts* 16-18, about 4.5 mm. long, 1.6 mm. broad, oblanceolate glabrous or minutely glandular, acute, with torn-ciliate margins. *Ray florets* about 20, the rays 4 mm. long, 1 mm. broad, lavender. *Receptacle* 2.5 mm. broad, 2.2 mm. high, broadly conical, rather deeply pitted. *Fruit* 2-2.2 mm. long, 1.3 mm. broad, oblong, flat, brown; body bearing small tubercles centrally, and laterally expanded into a wing-like irregularly incised margin. Pappus conspicuous.

Habitat: Forest country in well-drained situations.

Range: South-eastern Queensland.

Specimens examined:

Queensland: Robert's Plateau, near Moran's Falls, 2.1912, C. T. White (BRI); Robert's Plateau, National Park, "herb growing on rock faces in open forest, flowers lavender", 28.5.1929, C. T. White, n. 6078 (BRI, holotype and 5 paratypes, NSW, MEL); Fort Buchanan, about 1500', "herb, common in damp rocky crevices. Ray florets deep lavender, disc florets yellow", 16.4.1938, D. A. Goy and L. S. Smith, n. 263 (BRI).

The fruit of this species is unique in that the margin is irregularly extended into thick lobes, which are variable in number, size and position. The tubercles on the body and the relatively large pappus are characters indicating an affinity with *B. melanocarpa*, and it is interesting to note that the typically smooth margins of the latter species may sometimes be produced into tubercles. The general shape of the fruit of the two species is, however, quite distinct, those of *B. ascendens* bearing a superficial similarity to the flat winged fruit of *B. aculeata*. Vegetatively there is a strong resemblance to *B. Nova-Anglica* though the leaves of *B. ascendens* are typically broader.

A further specimen was examined bearing the label "Bright, a small white composite, 30.9.1926, A. Morris (NSW)", but attempts to trace this locality have been unsuccessful, and the record is not included in the list of specimens examined. This specimen differs vegetatively from the Queensland specimens in the presence of radical leaves up to

5.5 cm. long, which with the lower cauline leaves, are pinnatifid distally, the segments sometimes bearing one or more small teeth. The fruits, however, agree satisfactorily except that they are broad-linear in outline.

18. BRACHYCOME MICROCARPA F. Muell., Frag. phytog., 1 (1858), 50.

(Text-figs. 38, 44; Plate vi, map 15.)

Synonymy: *B. discolor* C. Stuart ex Benth., Fl. Aust., iii (1866), 520.

Lectotype: Brisbane River, 7.1855, F. Mueller (MEL).

Lectoparatype: *1.c. (MEL).

An ascending or weakly erect perennial, frequently with no main stem, up to 58 cm. high, more or less glandular-pubescent, seldom glabrous. Radical leaves, when present, up to 7.5 cm. long, orbicular or spatulate, pinnatifid or crenate, petiolate. Cauline leaves up to 7 cm. long, 2 cm. broad, narrow to ovate-cuneate or orbicular, pinnatifid to pinnatisect or crenate, sometimes almost palmate. Lower leaves usually petiolate, the segments acute, linear to broad linear, up to 8 mm. long, 2.5 mm. broad. Upper leaves sessile, a few on each plant opposite. *Peduncles* naked. *Capitula* 1-60, 3.5-8 mm. diameter. *Involucral bracts* 10-14, 2-3 mm. long, 1 mm. broad, narrow obovate, obtuse to sub-acute, with torn-ciliate margins. *Ray florets* 15-40, the rays 4-5 mm. long, 1 mm. broad, white or bluish. *Fruit* 1-1.8 mm. long, 0.7-0.9 mm. broad, dark brown to black, obovate-cuneate, flattened, laterally smooth, tuberculate on the central area of each face, with a few scattered glandular hairs on the tubercles. Pappus short, white.

Habitat: Forest land, in well-drained situations.

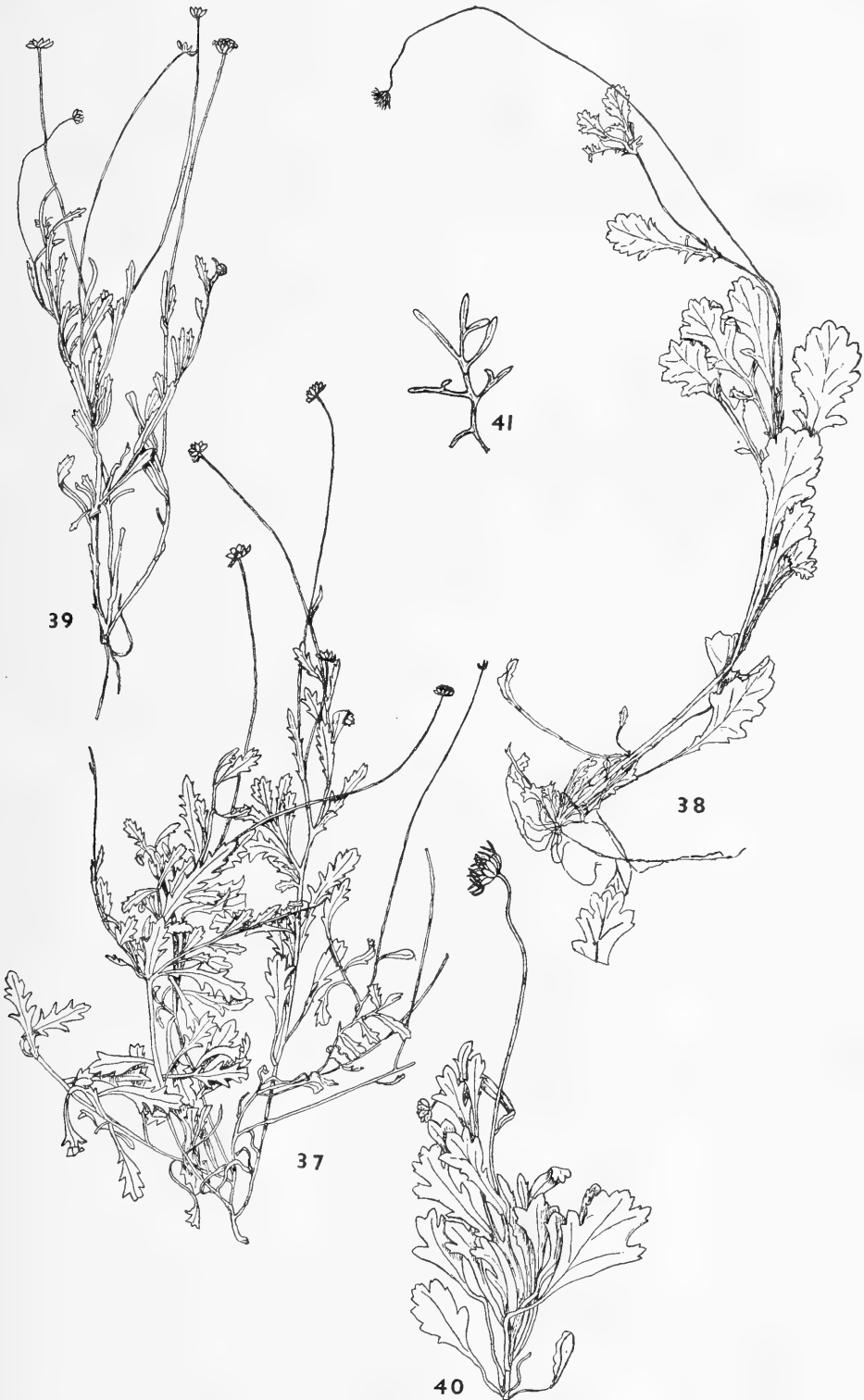
Range: Coastal region of eastern Australia from Bowen to Newcastle.

Specimens examined:

Queensland: Bowen (MEL); Burnett, R. (MEL); Wide Bay to Archers,* 10.8.1843, 12.8.1843, 16.8.1843, L. Leichhardt (MEL); *Wide Bay, Leichhardt (NSW); Gympie, F. H. Kenny (BRI); Petrie, Moreton district, "in open forest. Disc yellow, ray white or bluish", 2.1931, S. T. Blake (BRI); Ipswich, T. F. Hall (BRI); Bunya Mts., 10.1919, C. T. White (BRI); *Moreton Bay, F. Mueller (MEL); Brisbane River, 7.1855, F. Mueller (MEL, lectotype, lectoparatype); ridges about Brisbane, 3.1875, F. M. Bailey (BRI); One Tree Hill, near Brisbane, *6.10.1907, C. T. White (BRI); 10.1919, W. D. Francis (BRI); Taylor Range, 7.1916, C. T. White (BRI); Taylor Range, "in open eucalypt forest. Common on rocky slopes, 500'-700'", 24.8.1930, C. E. Hubbard (BRI); Indooroopilly, 11.1908, C. T. White (BRI); *Ormeau, N. Michael, n. 1882 (BRI); Logan, n. 345 (MEL); Bybera, "sandy soil", 3.9.1934, C. T. White, n. 10143 (BRI); Cunningham's Gap, main range, "grassland in Eucalypt forest" (BRI); *Thulimbah, "granite belt", 2.1934, C. Schindler (BRI); 1 mile south of Dalveen, "light grey podsol on granite. Slender, erect herb. Leaves pale green above, purple beneath, ray florets mauve, disc florets yellow", 21.11.1946, S. L. Everist and L. J. Webb (BRI); Stanthorpe, 7.1907, J. L. Boorman (NSW); *Stanthorpe, 10.1906, H. Wright (BRI); Stanthorpe, Davidson, n. 41 (BRI); *Ruby Creek, Stanthorpe, "in shallow sandy soil with granite outcrops. Herb with few radical leaves and erect, branching flowering stems. Ray florets mauve, disc florets yellow", 23.11.1946. S. L. Everist and L. J. Webb (BRI); Ballandean, 11.1944, M. S. Clemens (BRI); Wyberba, "among rocks in granite hills", 13.10.1933, C. T. White, n. 9378 (BRI); Bokkara Creek, 22.12.1846, L. Leichhardt (MEL); Mt. Mistake, "rocky slopes in open Eucalypt forest with *Themeda* and *Poa*, etc.", 1.800', 24.11.1930, C. E. Hubbard, n. 523 (BRI).

New South Wales: Drake, 6.1913, J. Richards (NSW); Tenterfield, 30.10.1886, E. Betche (NSW); Emmaville, 10.1901, 6.1904, J. L. Boorman (NSW); Tent Hill, 12.1910, J. B. Cleland (AD); Casino, 6.1891, W. Bauerlen (NSW); 4.1896, E. Betche (NSW, MEL, AD); Richmond River, 4.1896, E. Betche (BRI), C. Fawcett (MEL, NSW); *Clarence River, ? F. Mueller (MEL); Clarence R., Beckler (MEL); Ramornie, 3 miles north-west of Copmanhurst, 7.1922, W. F. Blakely and D. W. C. Shires (NSW); Smith's Creek, 7 miles north-east of Ramornie, 8.1922, W. F. Blakely and D. W. C. Shires (NSW); Orara River, 10 miles south of Ramornie, 7.1922, W. F. Blakely and D. W. C. Shires (NSW); Mt. Mullengen, 7.1922, W. F. Blakely and D. W. C. Shires (NSW); Jennings, 12.1903, J. H. Maiden and J. L. Boorman (NSW); New England, C. Stuart, n. 271 (MEL, lectotype and 3 lectoparatypes of *B. discolor*); Yamba, Clarence Heads, 11.1941, J. McComish (NSW); Crescent Head, "Sea Cliffs", 4.10.1941, Consett Davis (NSW, BRI); Manning River, 12.1.1899, 12.99, E. Cheel (NSW); Woodburn, 7.1859, 8.1896, W. Bauerlen (NSW); *Weston, 3.1912, V. C. Davis (NSW).

Mueller cites as the type locality "in dry meadows (especially mountainous) of subtropical Eastern Australia". From the syntype specimens available, one from the Brisbane River, collected and labelled by Mueller, was selected as lectotype, and though



Text-figures 37-41. Habit studies. $\times \frac{1}{2}$.
 37, *B. ascendens* (holotype). 38, *B. microcarpa* (lectotype). 39, *B. Nova-Anglica* (holotype). 40, *B. melanocarpa*. 41, *B. multifida* var. *dilatata*. Leaf.

the specimen is somewhat larger than most of those examined, the characters shown agree quite satisfactorily with the original description.

Both specimens mentioned by C. Stuart in his original description of *B. discolor* have been examined, and a lectotype nominated, though the species itself has been reduced to synonymy in *B. microcarpa*. The glabrous nature of the plants, recorded by Stuart, is more apparent than real, and careful examination of his syntype material shows them to be sparsely glandular distally. The main character on which *B. discolor* was based is the purple coloration of the lower leaf surfaces when fresh. This character has been noted by the author in several different genera of the Compositae and also of the Goodeniaceae. It is not a constant character but one which is probably correlated with some very local mineral salt deficiency, normal plants being found within a few feet of conspicuously purple ones.

The shape and structure of the fruit are constant, though a small variation in size occurs. It is in the leaves, however, that striking differences in shape occur. The upper cauline leaves are very similar in all specimens, being sessile and acutely toothed, and displaying a character unique in this genus in that many of them are opposite. In a comparatively large series no specimens were examined in which all the leaves were alternate. Complete gradation in shape of the lower cauline leaves is found, from the toothed or pinnatifid leaves typical of specimens from the north coast of New South Wales and elsewhere, to the orbicular and pinnatisect ones found in southern Queensland. All intermediate shapes are found, apparently with no geographical basis.

In characters of the fruit there is indication of fairly close affinity between *B. microcarpa* and *B. basaltica*, those of both species being of the same normally somewhat flattened shape, with numerous tubercles and smooth margins. The presence of a small though definite pappus is, however, a distinctive feature of *B. microcarpa*, and in all the fruits of *B. basaltica* examined no black ones were found.

19. BRACHYCOME NOVA-ANGLICA SP. NOV.

(Text-figs. 39, 45, 46; Plate vi, map 15.)

Holotype: Dumaresq Creek, near Armidale, "forest land", 23.11.1941, G. L. Davis (NSW).

Paratypes: Two, i.c. (MEL, NSW).

Herba perennis, ascendens, ramosa, ad 34.5 cm. alta, satis glandulosa et septatopilosa. Folia caulina, ad 4.8 cm. longa, 9 mm. lata, oblanceolata, sessilia, dentibus apicem versus 2-9 acutis dentata. *Pedunculi* nudi aut uno in medio phyllo. *Capitula* 1-24, transverse lata 6 mm. *Involucri phylla*, 16, 3.1-4 mm. longa, 1-1.5 mm. lata, angustobovata, obtusa-subacuminata, margine fimbriato-ciliata, dense glandulosa. *Flores radii* circiter 23, ligulis 6 mm. longis, 1.5-2 mm. latis, albis-violaceis. *Receptaculum* 1.5-1.7 mm. latum, 1-1.2 mm. altum, conicum, altis punctis. *Achaenia* 1.7-2.1 mm. longa 0.8-1 mm. lata, nigra, obovata, grossa, compressa, plane utroque tuberculata, margine glabra. Pappus mic. sufflavus.

Ascending branching perennials up to 34.5 cm. high, moderately densely glandular and septate-hairy. Leaves cauline, up to 4.8 cm. long, 9 mm. broad, oblanceolate, sessile, bearing 2-9 acute teeth, usually distally. *Peduncles* naked or with a single median bract. *Capitula* 1-24, 6 mm. diameter. *Involucral bracts* 16, 3.1-4 mm. long, 1-1.5 mm. broad, narrow-obovate, obtuse to sub-acute, with torn-ciliate margins, and densely glandular. *Ray florets* about 23, the rays 6 mm. long, 1.5-2 mm. broad, white to violet. *Receptacle* 1.5-1.7 mm. broad, 1-1.2 mm. high, conical, deeply pitted. *Fruit* 1.7-2.1 mm. long, 0.8-1 mm. broad, black, obovate, thick, flattened, conspicuously tuberculate on each face with smooth margins. Pappus microscopic, straw-coloured.

Habitat: Forest land on slopes, frequently among boulders.

Range: Northern tablelands of New South Wales.

Specimens examined:

New South Wales: Mt. Lindesay, 14.4.1914, H. M. R. Rupp (NSW); Tingha, "amongst loose stones", J. L. Boorman (NSW); Ebor Falls, New England, "forest land", 31.1.1941, G. L. Davis (NSW); Serpentine R., "forest land", 31.1.1941, G. L. Davis (NSW, BRI, MEL); Ben Lomond, 12.1899, J. H. Maiden (NSW); Backwater, near Guyra, "forest land", 23.4.1941, G. L. Davis (NSW); Mt. Pleasant, Backwater, 12.1945, N. McKie (NSW); Mt. Duval, "towards base", 9.3.1946, A. B. Smythe (NSW); Blue Hole, near Armidale,

"forest slopes", 15.4.1941, Consett Davis (NSW); Blue Hole, 28.4.1941, M. Cumpston (NSW); Dumaresq Creek, Armidale, "forest land", 23.11.1941, G. L. Davis (MEL, holotype; NSW, MEL, paratypes); Dangar's Falls, near Armidale, 4.1941, B. Bassinett (NSW); Moonbi, 23.11.1886, E. Betche (NSW); Nundle, 6.1906, J. H. Maiden and J. L. Boorman (NSW).

In the series examined no departure from the typical condition was noted except for small variations in size of leaves and fruit.

This species is exceptionally well defined, and can be identified with certainty in the absence of fruit. It is most closely allied to *B. melanocarpa* both in vegetative features and fruit structure, but the general shape of the leaves in both species is quite distinct, and the microscopic pappus makes diagnosis quite certain in immature fruit in which the characteristic shape is not yet attained.

The size of the fruit is intermediate between that of *B. melanocarpa* and *B. microcarpa*, but in the constant presence of smooth margins and somewhat flattened appearance shows definite affinities with *B. microcarpa*. It would seem that in structure as well as range, *B. Nova-Anglica* occupies an intermediate position between these two species.

20. BRACHYCOME MELANOCARPA Sond. F. Muell., *Linnaea* xxv (1852), 476.

(Text-figs. 40, 47, 48; Plate vi, map 15.)

Lectotype: *Murray R., F. Mueller (MEL).

Lectoparatypes: *Two, l.c. (MEL).

Weakly erect to erect branching (?) perennials up to 45 cm. high, sparsely to moderately densely glandular and septate hairy. Radical leaves only present in young plants, about 7 cm. long, usually oblong-cuneate with broad acute lobes, almost crenate in appearance. Cauline leaves up to 5.5 cm. long, narrow to oblong-cuneate, irregularly toothed, pinnatifid or pinnatipartite with acute segments, petiolate when oblong cuneate, otherwise sessile. *Peduncles* leafy proximally. *Capitula* 1-80, 0.7-1 cm. diameter. *Involucral bracts* 12-14, 4-5 mm. long, 1.8-3 mm. broad, obovate, entire or slightly torn-ciliate, obtuse to sub-acute, glandular. *Ray florets* about 20, the rays 7 mm. long, 2.5 mm. broad, white to bluish purple. *Receptacle* 3.5 mm. broad, 1.5 mm. high, conical, deeply pitted. *Fruit* 2-2.5 mm. long, 1 mm. broad, obovate, turgid and subcylindrical at maturity, densely tuberculate on each face, the margins frequently inconspicuous, usually smooth but sometimes more or less tuberculate. Pappus white, conspicuous.

Habitat: Grassland.

Range: Western districts of Queensland and New South Wales to north-eastern and south-eastern South Australia.

Specimens examined:

Queensland: Murweh, Warrego R., 9.1916, R. Cameron (BRI); Cunnamulla, 3.4.1941, C. T. White, n. 11823 (BRI); Curragh, near Cunnamulla, 620', "on flat open country with short mixed herbage, originally forest", 4.1.1931, C. E. Hubbard and C. W. Winders, n. 6238 (BRI); Gilruth Plains, Cunnamulla, "sandy loam", 10.2.1941, R. Roe (CSIR); *Gilruth Plains, Cunnamulla, "brown loam soil, Mitchell grass country", 21.7.1941, R. Roe (CSIR); Gilruth Plains, Cunnamulla, "greyish brown soil", 11.6.1942, G. H. Allen (CSIR); Gilruth Plains, Cunnamulla, "heavy brown clay soil, open plain country", 6.1.1946, G. H. Allen (CSIR); *Queensland border north of Bourke, 1884, Henry (MEL); St. George, 5.1894, J. Wedd (BRI); Wyaga, Goondiwindi district, 9.1919, C. T. White (BRI).

New South Wales: Angledool, "black soil, flat country", 1.7.1913, C. T. Musson (NSW); *between 40 and 50 miles N.-W. of Collarenebri, 11.1911, S. W. Jackson (NSW); Gravesend, 2.1913, E. Breakwell (NSW); 20 miles S. of Walgett, "under trees of *E. bicolor*. Red brown loam", 1942, N. C. W. Beadle (NSW); Jew's Lagoon, 50 miles W. of Narrabri, W. F. Blakely (NSW); Mayvale, 14.4.1914, H. M. R. Rupp (NSW); *Balmoral, Gunnedah, 9.1910, J. W. Hodgson (NSW); near Carinda, "under trees of *E. populifolia*. Brown loam", 9.1942, N. C. W. Beadle (NSW, BRI, MEL); Gulargambone, 9.1886, Cardell (NSW); Bourke, 8.1896, J. H. Maiden (NSW); Bourke, "black soil", 3.1941, N. C. W. Beadle (NSW); Nultz and Joorale, north-western district, 9.1912, J. L. Boorman (NSW); Menindee, "*E. bicolor* woodland", 6.1942, N. C. W. Beadle (NSW); *Menindee, 15.10.1860, Vict. Exped. (MEL); Darling River, Dallachy (MEL); *Darling desert, F. Mueller (NSW, MEL); Murray River, F. Mueller (MEL, lectotype, lectoparatype).

South Australia: Strzelecki Creek, R. Tate (AD); Chorvilla, R. Murray, 1.1884, R. Tate (AD); Renmark, 3.10.1915, J. M. Black (JMB); R. Murray, 9.1911, Bunda (JMB).

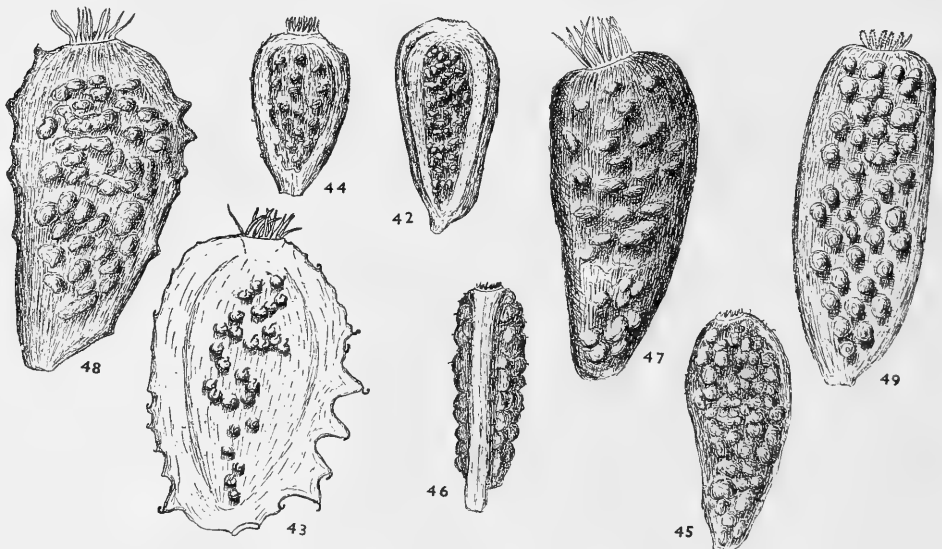
Only three syntype specimens being available, the largest was nominated lectotype, and the remaining two became lectoparatypes. Unfortunately none of them bear mature fruit, but the vegetative features exhibited leave no doubt as to their identity. The description of the fruit given is based on a reasonably long series of specimens conspecific with the type, and agreeing with the original description.

Although individual leaves show considerable variation, frequently among those on the same plant, the general appearance of the plant is relatively constant. The greatest contrast between individuals is seen when a young plant (? first year) in which radical leaves are present is compared with another bearing only cauline ones. In the former the radical and lower cauline leaves form a dense basal cluster, and are oblong cuneate, coarsely lobed and petiolate. With increase in size of the plant (? second year) the radical leaves die off and the cauline leaves exhibit the characteristic narrow-cuneate shape, are sessile and distally toothed.

The fruits are relatively large, turgid and subcylindrical with a white pappus. The tubercles on each face are usually very conspicuous, but in some cases they are less apparent than others. Certain of the Cunnamulla specimens show an interesting variation, in that the tubercles are pointed, very dense, and extend round the entire fruit. In most cases, however, a narrow smooth margin can be seen extending round the fruit.

The fruit are constructed on the same plan as those of *B. microcarpa* and show the same trends, but in *B. melanocarpa* these trends are carried further, and the resultant characters are more highly specialized. The tubercles, small in *B. microcarpa*, are here relatively immense, and, as noted above, sometimes extend round the entire fruit so that the smooth margin is no longer apparent. The flattened type of fruit has given place to a cylindrical one, and the pappus has increased in size. The entire fruit is roughly three times the size of that of *B. microcarpa*.

B. melanocarpa is essentially a western species and roughly may be said to begin where *B. microcarpa* leaves off. This would seem to indicate that these two species originated as geographic subspecies, and that the slight overlap in their range is a secondary occurrence.



Text-figures 42-49. Fruit. $\times 17$ approx.

- 42, *B. basaltica*. 43, *B. ascendens*. 44, *B. microcarpa*. 45, *B. Nova-Anglica*.
 46, *B. Nova-Anglica*. 47, *B. melanocarpa*. Fruit with smooth margins.
 48, *B. melanocarpa*. Fruit with tuberculate margins. 49, *B. multifida*.

21. BRACHYCOME MULTIFIDA DC., Prod. v (1836), 302.

Glabrous, robust or weakly erect ? annuals, branching from the base with no main stem, up to 44 cm. high. Leaves cauline, up to 7 cm. long, once or twice pinnatisect to pinnatipartite, the segments 7-10, up to 3.5 cm. long, 0.5-4 mm. broad, narrow- to linear-subulate, oblanceolate or cuneate, acute, entire, toothed or pinnatisect. *Peduncles* naked or with a single filiform bract. *Capitula* 1-100, 4 mm. diameter. *Involucral bracts* 18-22, 2.5-3.6 mm. long, 1-1.9 mm. broad, oblanceolate, obtuse to subacute, the margins minutely ciliolate. *Ray florets* 16-29, the rays 7-10 mm. long, 1.3-1.6 mm. broad, mauve, pink or white. *Receptacle* 1.2-2.9 mm. broad, 0.6-1.3 mm. high, conical, slightly to moderately pitted. *Fruit* 1.9-2.4 mm. long, 0.8-1 mm. broad, dark brown to black, turgid and slightly flattened, narrow-cuneate to cuneate, tuberculate with narrow smooth margins; each tubercle surmounted by a usually forked hair. Pappus white, short, spreading, the bristles of unequal length and grouped in bundles, each bundle having a plumose appearance.

Key to the varieties.

1. Leaf-segments narrow linear-subulate var. *a multifida*.
 1.* Leaf-segments broad-linear oblanceolate or cuneate var. *β dilatata*.

Brachycome multifida DC., var. *a multifida* comb. et stat. nov.

(Text-fig. 49; Plates vi, map 16; ix, 1.)

Lectotype: "Peel's Range, interior of N.S.W., Lat. 34° S., 11.6.1817", A. Cunningham (GENEVA).
Lectoparatype: l.c. (GENEVA).

Haptotypes: *Peel Range, 1817, A. Cunningham (MEL, BRI).

Leaves up to 5.7 cm. long, pinnatisect. Segments linear-subulate, up to 2.2 cm. long, the proximal segments shorter, frequently filiform.

Habitat: Open forest or grassland.

Range: South-eastern Queensland, through New South Wales to northern Victoria.

Specimens examined:

Queensland: Bybera, "sandy soil, mauve flowers", 5.5.1934, C. T. White, n. 10046 (BRI); Bybera, "sandy soil, pink flowers", 3.9.1934, C. T. White (BRI); Inglewood, 8.11, J. L. Boorman (NSW); Stanthorpe, "in Eucalypt forest, at foot of granite mountain in quartzite grit, amongst granite boulders, 2656 ft.", 11.3.1931, C. E. Hubbard, n. 5726 (BRI).

New South Wales: *Emmaville, 10.1901, J. L. Boorman (NSW); *Sugar Loaf, 5 m. W. of Ramornie, 7.1922, W. F. Blakely and D. W. C. Shiress (NSW); *Brickmaker's Creek, 5 m. W. of Ramornie, 7.1922, W. F. Blakely and D. W. C. Shiress (NSW); Clarence R., 1881, Stackhouse (MEL); New England, C. Stuart (MEL); Warialda, "small upright-growing annual of a weak habit", 7.1905, J. L. Boorman (NSW); Howell, 12.1906, R. Hart (NSW); Howell, 12.1914, J. L. Boorman (NSW); Bingara, 9.1907, J. L. Boorman (NSW); *head of the Gwydir, Leichhardt (MEL); *Nandewar Mts., 11.1909, R. H. Cambage (NSW); Narrabri, 11.1899, J. H. Maiden (NSW); Pilliga forest, 9.1913, E. H. F. Swain (NSW); Warrambungle Ranges, 10.1899, W. Forsyth (NSW); Harvey Range, Peak Hill, 10.1905, 10.1905, J. L. Boorman (NSW); plains near Dubbo, 9.1883, E. Betche (NSW); Dubbo, "abundant in paddocks", 1883, E. Betche (NSW); Dubbo, 9.1900, 12.1907, 6.1914, J. L. Boorman (NSW); Dubbo, "small erect annual, flowers white, growing at the sandhills, amongst *Dillwynia juniperina*, *Acacia gnidia*, etc.", 11.1905, J. L. Boorman (NSW); Mudgee, 1870, Taylor (NSW); *Bathurst, 1884, Stephenson (NSW); *Gungal, near Merriwa, 9.1904, J. L. Boorman (NSW); Raymond Terrace, 5.1918, E. Cheel (NSW); *West Maitland, 12.1886, Sarrington (NSW); West Maitland, 2.9.1912, N. Crouch (NSW); Glenori, 3.12.1938, W. F. Blakely (NSW); *Windsor, 10.1914, D. Johnstone (NSW); *Parramatta, W. W. Woolls (MEL); Castlereagh, W. W. Woolls (MEL); "barren hills near the depôt, Lachlan R.", 4.1817, A. Cunningham, n. 326 (MEL); *Peel Range, 1817, A. Cunningham, n. 337 (MEL, BRI, haptotypes); Kamarach, 17.10.1917, W. R. A. Baker (NSW).

Victoria: Murray R., F. Mueller (MEL); Murray R., Hergott (MEL); Murray Desert, ? F. Mueller (MEL); Murray pine scrub, Lower Murray R., 10.1886, C. French (MEL); Loddon R., F. Mueller (MEL); Talbot (MEL).

The lectotype of this species is at present in De Candolle's Herbarium, Geneva, and consequently was not available for examination. The author is greatly indebted to Professor Baehni of that Institution for a fruit and floret from syntype material as well as an excellent photograph of the herbarium sheet on which De Candolle's two specimens are mounted (Pl. ix, 1). In addition to this material, specimens have been found in the National Herbarium, Melbourne, and the Brisbane Herbarium, which were collected at

the type locality by Alan Cunningham, presumably at the same time as the syntype series. It is doubtful whether these specimens were ever examined by De Candolle, and consequently have been nominated haptotypes. Unfortunately they are in a fragmentary condition, and are unaccompanied by fruit, but as there is no doubt as to their identity they have been used as a basis of comparison for all specimens.

In the original description De Candolle observes, "closely similar to Fig. 207, Labillardière, but the fruits are certainly not ciliate, and the lobes of the leaves are more slender and more acute". The figure referred to is of *Bellis ciliaris* Labill., to which there is a strong superficial similarity in some specimens.

Variation within this variety is slight, and confined to small differences in the lengths of the leaf-segments.

Brachycome multifida DC., var. β *dilatata* Benth. Fl. Aust., iii (1866), 520.

(Text-fig. 41; Plate vi, map 16.)

Synonymy: *B. glabra* Benth., Enum. Pl. Hueg. (1837), 59. *B. tenera* Benth., Enum. Pl. Hueg. (1837), 59.

Haptotype: "New Holland", Ferd. Bauer (MEL).

Leaves up to 7 cm. long, frequently twice pinnatisect or pinnatipartite; primary segments up to 2.8 cm. long; ultimate segments acute, oblanceolate to broad-cuneate, more or less abruptly tapered to the acute apex.

Habitat: Grassland.

Distribution: Central coastal area of New South Wales, coast and mountains of southern Victoria.

Specimens examined:

New South Wales: Gloucester Buckets, 9.1897, J. H. Maiden (NSW); 5.1946, A. B. Smythe (NSW, MEL, BRI, AD, PERTH); *Port Stephens, 8.1911, J. L. Boorman (NSW); West Maitland, 3.1909, A. Brewster (NSW); Newcastle, South Downs, 26.9.1842, L. Leichhardt (MEL); Newcastle, 8.1898, J. H. Maiden (NSW); Newcastle, 10.1902. *6.1907, R. H. Cabbage (NSW); Newcastle, 14.10.1911, A. A. Hamilton (NSW); West Wallsend, 10.1901, R. H. Cabbage (NSW); *Wallsend, 10.1899, J. L. Boorman (NSW); Wiseman's Ferry, 4.1908, J. L. Boorman (NSW); *New Holland, Ferd. Bauer (MEL, haptotype *B. tenera*).

Victoria: McIvor (MEL); *Mt. Macedon (BRI); Mt. Macedon (MEL); Mt. Macedon, C. Walter (MEL); *Plenty R., "growing in moist shady position in *Eucalyptus* forest. Rays pale blue", 10.1943, L. S. Smith (BRI); Mount Disappointment, 10.1852, F. Mueller (MEL); Wandong Ranges, 10.1898, C. Walter (MEL); Dandenong Ranges, 1.1853, F. Mueller (MEL); Dandenong Ranges, 1.05, W. S. Brownscombe (MEL); *Dandenong Ranges, 4.1911, J. Staer (MEL); Snowy R., 10.1904, C. H. Grove (MEL); Orbost, 9.1900, E. E. Pescott (MEL); Lake Wellington, 2.1855, F. Mueller (MEL); Mouth of Gellibrand R., 3.1874, F. Mueller (MEL, NSW); *Victoria Ranges, 11.1853, F. Mueller (MEL); Rocky places near the top of the Victorian Ranges, C. Wilhelm (MEL); Grampians (MEL); Grampians, 11.1899, C. Walter (MEL); *Grampians, 11.1900, H. B. Williamson (MEL); *Grampians, 11.1903, H. B. Williamson (BRI); Grampians, St. Eloy D'Alton, n. 10 (MEL); *Greenbow, 4.1911, J. Staer (NSW); Aust. Felix, F. Mueller (MEL).

In his original description of *B. tenera*, Bentham does not cite a locality, merely giving the collector "Ferd. Bauer". Authentic syntype material being unavailable in Australia, a specimen originally from Robert Brown's collection which bears the caption "New Holland, Ferd. Bauer", was nominated haptotype. This specimen consists of some separate leaves, a flowering capitulum, and a few fruits, and probably represents portions removed from Bauer's original specimen. Bentham subsequently (1866) reduced this species to a variety, var. *dilatata*, of *B. multifida*. In this instance a definite locality is quoted and a different collector (viz., "Hunter's R., R. Brown"), so that the syntype specimens of *B. tenera* and *B. multifida* var. *dilatata* are different. The synonymy is accepted partly on Bentham's authority, and partly because the fruits of the haptotype agree satisfactorily with those of *B. multifida* var. *multifida*.

The variety *dilatata*, like any naturally occurring population, is a somewhat variable series oscillating about a hypothetical mean point. It is fortunate, but entirely fortuitous, that most syntype specimens occupy a position in the neighbourhood of this point. In this instance, however, the haptotype is a variational extreme and consequently though a "type", is not vegetatively typical of the variety.

B. glabra was described by Bentham from material collected by Ferd. Bauer in Australia between 1802 and 1805, no definite locality being cited. Syntype material, if still extant, is probably in the British Museum, but attempts to obtain any information on this matter have been unsuccessful. There are, however, a number of specimens in the National Herbarium, Melbourne, identified by Mueller as *B. glabra*, which were subsequently examined by Bentham, who in the absence of any evidence to the contrary, presumably confirmed this diagnosis. These specimens do not agree well with type specimens of *B. multifida* var. *multifida* but do fall within the new varietal limits of var. *dilatata*, and consequently have now been included under this category.

Whereas var. *multifida* is remarkably constant in vegetative characters, a comparatively large series of specimens of var. *dilatata* shows considerable variation in the dimensions of the leaf-segments. On the one hand are the broad, apparently flaccid leaves, almost palmately divided, and on the other are leaves approximating in appearance to var. *multifida*, all intermediate conditions being found. The two varieties can be distinguished by the fact that the leaf-segments of var. *multifida* are always relatively long and narrow-linear, tapering imperceptibly to an acute apex, while those of var. *dilatata*, though very variable in relative proportions, are comparatively broad proximally and abruptly tapered distally.

Certain specimens show a strong similarity to *B. melanocarpa* and determination may be a matter of conjecture when only flowers or young fruit are present. The characteristic appearance of the pappus is, however, distinguishable at a very early stage, and in no other species has this almost plumose appearance been noted.

A close affinity exists between *B. multifida* and *B. melanocarpa*, the fruit in some cases being indistinguishable except for details of the pappus noted above. This similarity is particularly striking in certain specimens of *B. multifida* var. *dilatata*, in which the leaves approach closely to those of the *B. melanocarpa* type.

B. multifida var. *dilatata* has a more extensive range than var. *multifida* and is mainly coastal in its distribution, whereas the latter variety is found chiefly in the northern tablelands and western districts of New South Wales.

4. Superspecies ACULEATA.

22. BRACHYCOME ACULEATA (Labill.) Less. Syn. Comp. 192, 1832.

(Text-fig. 58; Plates vi, map 17; x, 1-2.)

Synonymy:

- Bellis aculeata* Labill., Pl. Nov. Holl. (1806), 55.
Brachycome Billardieri Cass., Dict. Sci. Nat. V. Suppl. (1817), 63.
Brachycome stricta DC., Prod. V (1836), 306.
B. scapiformis DC., l.c.
B. scapiformis DC. var. *puberula* DC., l.c.
B. scapiformis DC., var. *glabra* DC., l.c.
B. Sieberi DC., l.c.
B. Sieberi DC., var. *Gunnii* DC., l.c.
B. leucanthemifolia Benth., Enum. Pl. Hueg. (1837), 60.
B. oblongifolia Benth., l.c.
B. glauca Walp., Linnaea xiv (1840), 315.
B. cuneifolia Tate, Roy. Soc. S.A., xi (1889), 83.

Leototype: *Bellis aculeata* Labill., New Holland, Labillardière (GENEVA).

Erect or ascending more or less branched perennials with one to several stems, up to 62 cm. high with a glandular indumentum variable in development. Basal rosette of radical and lower cauline leaves present in young plants, the leaves of which are oblanceolate to spatulate, tapering strongly proximally, rarely becoming petiolate, up to 10 cm. long, 2 cm. broad, crenate to acutely lobed distally. Upper cauline leaves sessile, linear, broad-linear or cuneate, acutely and irregularly toothed distally, occasionally pinnatifid, rarely entire. *Peduncles* slender or robust, almost scape-like in young plants, leafy proximally. *Capitula* 1-45, up to 1.8 cm. across involucrel bracts. *Involucrel bracts* about 20, up to 8 mm. long, 2 mm. broad, narrow-elliptical to elliptical or lanceolate, acute, microscopically torn-ciliate, glandular. *Ray florets* 27-35, up to 8 mm. long, 2 mm. broad, white, lilac or blue, *Receptacle* up to 3 mm. high, 3 mm. broad, broadly conical, moderately pitted. *Fruit* 3-4 mm. long, 2.2-3 mm. broad, flat,

greenish-brown, obovate, the body bearing a few microscopic glandular hairs, the wing almost entire to irregularly and incompletely dissected. Pappus at least equal to the notch between the wings.

Habitat: Well drained to dry situations.

Range: South-eastern Queensland, coast and tablelands of New South Wales, with a few records from the north-western plains. Throughout Victoria to south-eastern South Australia. Widespread in Tasmania.

Specimens examined:

Queensland: Timba, plains of the Condamine, Pemberton Hodgson (MEL); Maroon, 21.12.1935, N. Michael (BRI).

New South Wales: *Gwydir R., 14.12.1846, ? A. Cunningham (MEL); Bolivia, 2.1914, H. M. R. Rupp (NSW); Glen Innes, 1.1911, F. H. Kenny (BRI); Glen Innes, 6.1917, J. L. Boorman (NSW); 7 miles W. of Guyra, 18.2.1941, Consett Davis (NSW); *Backwater, Guyra, 23.3.1941, G. L. Davis (NSW, BRI); Rose Hill, Guyra, 24.2.1941, Consett Davis (NSW); Ebor Falls, 31.1.1941, G. L. Davis (NSW, MEL, AD, BRI); Point Lookout, New England, 31.1.1941, G. L. Davis (NSW, MEL, AD, BRI); *Yaroona, Snowy Ranges, 31.1.1941, G. L. Davis (NSW, MEL, BRI); Coff's Harbour, 3.1912, J. L. Boorman (NSW); *Walcha, 16.10.1899, J. F. Campbell (NSW); *Castlereagh R., ? F. Mueller (MEL); Coolabah, 1901, R. N. Peacock (NSW); Nevertire, 30.9.1886, E. Betche (NSW); Mudgee line, 10.1893 (NSW); Orange, 11.1906, J. L. Boorman (NSW); Sunny Corner, 11.1899, J. L. Boorman (NSW); Mt. Blaxland to Rydal, 4.1909, J. H. Maiden and R. H. Cambage (NSW); *Wallerawang, 11.1899, J. H. Maiden (NSW); Wallerawang, "grassland, stony places", 12.1917, J. L. Boorman (NSW); Bathurst, 1884, Stephenson (NSW); Bathurst, 1929, R. G. May (NSW); Hartley Vale, 15.1.1892 (NSW); *Hartley Vale, 11.1913, A. A. Hamilton (NSW); Rockley, 11.1906, J. L. Boorman (NSW); Trunkey, 11.1918, J. L. Boorman (NSW); Jenolan Caves, 11.1899, W. F. Blakely (BRI, NSW); Jenolan Caves, 12.1899, W. F. Blakely (NSW); *Parramatta (MEL, NSW); Cabramatta district (MEL); Richmond, 1802-5, Robert Brown (MEL); Richmond, 12.5.1916, C. T. Musson (NSW); Palm Beach, 5.1916, H. E. Ellen (NSW); *Port Jackson, 1802-5, Robert Brown (MEL); Mt. Werong, 4.12.1911, R. H. Cambage (NSW); *Wombeyan Caves, 10.1905, R. H. Cambage (NSW); Rocky places near Berrima, 2.1865 (MEL); Berrima, 22.4.1889, J. J. Fletcher (NSW); *Berrima, 7.1906, J. L. Boorman (NSW); Wingello, 12.1917, J. L. Boorman (NSW); *Mt. Ettrema, 20 miles S.W. of Nowra, 16.11.1941, F. A. Rodway (NSW); *Shoalhaven Heads, low lying flat land, 21.6.1939, F. A. Rodway (NSW); *Milton, 11.1900, Warden (NSW); Nerriga, 1.1915, J. L. Boorman (NSW); Gudenby, Queanbeyan, 4.500', 14.1.1912, R. H. Cambage (NSW); Bimberi Peak, Upper Cotter R., Queanbeyan, 6,200', Granite, 15.1.1912, R. H. Cambage (NSW); Coree, Queanbeyan, 4,500', 10.12.1911, R. H. Cambage (NSW); Upper Cotter, Queanbeyan, 14.1.1912, R. H. Cambage (NSW); between Sassafras and Ettrema, Moorland, 5.1.1947, F. A. Rodway (NSW); *Charlie's Forest, near Braidwood, 3.1909, J. L. Boorman (NSW); Bendithera, 40 miles S. of Braidwood, 12.4.1941, F. A. Rodway (NSW); Batlow, 10.1916, J. L. Boorman (NSW); Yarrangobilly Caves, 2.1897, E. Betche (NSW); Yarrangobilly Mt., near summit, 12.1.1944, J. Vickery (NSW); Kiandra, 2.1897, E. Betche (NSW); Kiandra, 12.1901, W. Forsyth (NSW); Adaminaby-Talbingo Rd., 3,000', 4.12.1943, S. Copland (NSW); Jindabyne, 1.1899, J. H. Maiden and W. Forsyth (NSW); Nimmitibel, 12.1916, J. L. Boorman (NSW); Nimmitibel to Tantawonglo Mts. (NSW); Twofold Bay, 9.1860, F. Mueller (MEL); *Mt. Kosciusko, 12.1924, 1.1930, T. Harris (NSW); Sawpit Crk., Mt. Kosciusko, 1.1899, J. H. Maiden and W. Forsyth (NSW); Mt. Kosciusko, tree-line to 7,000', 1.1899, J. H. Maiden and W. Forsyth (NSW, MEL); *Mt. Kosciusko, 2.1901, R. Helms (NSW); Mt. Kosciusko, Bett's Camp, 16.2.1914, J. H. Maiden (NSW).

Victoria: Genoa district, 3.1885, W. Baiieren (MEL); *Ingeegoodbee (Trib. of Snowy R.), 3.1940, W. Hunter (MEL); Orbest, 8.1899, E. E. Prescott (MEL); Cape Conran, 4.1.1911, P. R. H. St. John (MEL); *Neumerella, 28.5.1902, C. Grove (MEL); Ensay, Tambo R., 6.10.1926, A. Morris (NSW); *Merriman's Crk., F. Mueller (MEL); Omeo, 14.1.1940, F. J. Rae (MEL); *Mt. Feathertop, 5,000', 12.1917, A. J. Tadgell (MEL); *Buffalo Mts., 1.1899, C. Walter (NSW); *Buffalo Mts., 2.1904, ? F. Mueller (MEL); Mt. Buffalo, 4,300', Granite, 19.1.1913, R. H. Cambage (NSW); Mt. Buffalo, 12.4.1940, Wigan (MEL); Mt. Hotham, 1.1900, J. H. Maiden (NSW); Mt. Timbertop, Stony Summits, 3.1853, F. Mueller (MEL); Mt. Buller, 22.3.1853, F. Mueller (MEL); Mt. St. Bernard, 1.1900, J. H. Maiden (NSW); Mt. Mitchell (MEL); Delatite R., on high dry banks, 15.3.1853, F. Mueller (MEL); Mt. Barkley, 5,000', 1.1863, F. Mueller (MEL, NSW); top of Victorian Ranges, moist places, 1.1857, C. Wilhelm (MEL); King Parrot Creek, 4.1853, F. Mueller (MEL); Barber's Crk., 1.1898, J. H. Maiden (NSW); Barber's Crk., 9.1899, J. L. Boorman (NSW); Barber's Crk., 11.1899, H. J. Ramsay (NSW, BRI); Echuca, 12.1904 (MEL); Mt. Emu Crk., 11.1853, F. Mueller (MEL); Grampians, 11.1900, C. Walter (MEL); *Hall's Gap, Grampians, 12.1912, J. E. Tilden (MEL); *Wonderland, Grampians, 11.1920, J. W. Nudds (BRI); *Shire of Dimboola, Mallee Scrub, 23.9.1900, F. M. Reader (MEL); Shire of Dimboola, 30.9.1891, F. M. Reader (MEL); Mallee district, 10.1899, C. Walter; *Mallee District, N.W. Vict., St. Eloy D'Aiton (MEL).

Tasmania: Port Dalrymple, 1802-5, Robert Brown (MEL); Launceston, 11.1863 (MEL); *Hills above Launceston, 11.1863 (MEL); near Launceston, "marshy ground", 1.1867 (MEL); Penquite, 2.10.1841, R. Gunn, n. 168 (NSW); Penquite, 5.12.1842, R. Gunn, n. 1146 (NSW); Penquite, 11.11.1843 (MEL); *near Perth, 11.1848, F. Mueller (MEL); *South Esk, rocks, 7.11.1844, 17.12.1844, R. Gunn, n. 388 (NSW); South Esk, 24th Nov., ? C. Stuart (MEL); *South Esk, F. Mueller (NSW); *George's Bay, A. Simson (BRI); *George's Bay, 6.1892 (NSW); *Glen Leith, 18.10.1839, R. Gunn, n. 66 (NSW); Swanport to Swansea, 1.1902, J. H. Maiden (NSW); *Brighton, A. Simson (BRI); New Norfolk, 20.11.1840, R. Gunn, n. 66 (NSW); Risdon, 27.11.1840, Gunn, n. 168 (NSW); Bellerive, "sand dunes", 9.1892, L. Rodway (NSW); Bellerive, R. A. Black (RAB); *Grass Tree Hill, near Bellerive, 7.11.1921, R. A. Black (RAB); Bellerive, "sandy and rocky country, 50 ft.", 6.1929, F. H. Long (HO); Lindisfarne, 2.12.1922, R. A. Black (RAB); *Lindisfarne, "near sea level", 8.11.1936, A. M. Olsen (HO); Mt. Wellington, 12.1892, L. Rodway (NSW); Mt. Wellington, "amongst rocks near summit", ? F. Mueller (MEL); Mt. Wellington, 3.1910, E. Cheel (NSW); *Mt. Wellington, 2.4.1911, 7.2.1922, R. A. Black (RAB); near Organ Pipes, 3.1.1912, R. A. Black (RAB); *Mt. Wellington, 3,500', 2.2.1932, C. T. White, n. 8370 (BRI); *Mt. Wellington, 3.1940, Holloway (MEL); Cascades, 29.10.1921, R. A. Black (RAB); Hobart, 1838, T. Siemssen (MEL); Hobart, R. Gunn, n. 66 (NSW); *Hobart, "hillsides", 11.1870, S. G. Hannaford (NSW); *Hobart, 1909, F. H. Kenny (BRI); *Domain, Hobart, 3.11.1934, V. V. Hickman (HO); Hobart, 11.1923, 12.1923, A. H. S. Lucas (NSW); Knock Lofty, Gunn, n. 168 (NSW); Mt. Nelson. 1.1901, A. H. S. Lucas (NSW); Mt. Nelson, 1,000', 31.1.1947, F. A. Rodway (NSW); Mt. Nelson, R. A. Black (RAB); near Hobart, "sandy situation near sea level", H. D. Gordon (HO); *Blackman's Bay, 11.1929, L. Rodway (HO); Ridgeway, 1.1908, L. Rodway (HO); *Boomer, "light bush", 12.1943, W. M. Curtis (HO); Taylor's Bay, South Bruné Is., "tufted mats on banks by the sea", F. Mueller (MEL); Oyster Cove, D'Entrecasteaux Channel, 1.12.1852 (MEL); Lake St. Clair, R. A. Black (RAB); *National Park, "shady bank, roadside, 500 ft.", 23.1.1944, W. M. Curtis (HO); Gordon R., 14.12.1846 (MEL); Mt. King William, 31.12.1914, R. A. Black (RAB); Mt. Field East, 4,000', 3.1906, J. H. Maiden (NSW); Mt. Direction, 9.9.1923, R. A. Black (RAB); *Tasmania, W. H. Archer (NSW).

South Australia: Port Lincoln, R. Tate (AD, lectotype and lectoparatype of *B. cuneifolia*); between Coromandel Valley and Clarendon, 9.10.1939, J. B. Cleland (JBC); *Clarendon, 27.1.1881, J. M. Black (JMB); *Kangarilla, 9.10.1929, J. A. Cleland (JMB); Naracoorte, 10.1920 (JMB).

The population of plants now covered by the name *Brachycome aculeata* has suffered more vicissitudes in nomenclature than any other such group in this genus, as evidenced by the long synonymy.

Syntype specimens of *Bellis aculeata* Labill. are extant in the Natural History Museum, Paris, and in the De Candolle Herbarium, Geneva. The author is indebted to Professor Humbert for the following information with regard to the former: "a very bad specimen, with a single flowering capitulum, without fruits". An accompanying photograph bears out the first part of this comment. The specimen at Geneva, on the other hand, is in an excellent state of preservation with mature fruit, and a photograph shows it to resemble closely Labillardière's figure (Pl. Nov. Holl.).

Cassini, although he is the author of the generic name, never actually wrote "*Brachycome*" and "*aculeata*" in juxtaposition, and as Lessing was the first to make this combination it is attributed to him. Lessing's description is based on the specimens collected in "New Holland" by Labillardière and Sieber, but De Candolle did not agree that they were conspecific, and in 1836 he redescribed Labillardière's specimen of *Bellis aculeata* as *Brachycome stricta*, and erected a new species, *B. Sieberi*, for that collected by Sieber. Lessing's two syntypes were thus distributed between two new species, and the original epithet unjustifiably abandoned. Labillardière's specimen at Geneva is designated lectotype not only of *Bellis aculeata*, but of *Brachyscome Billardieri*, *Brachycome stricta* and *B. aculeata*, the same specimen having been used by the respective authors of these names.

Through the courtesy of the Director of the De Candolle Herbarium, Professor C. Baehni, the author has been furnished with photographs, florets and young fruit of syntype specimens of *B. stricta* and *B. Sieberi*. The latter specimen of *B. Sieberi* is of rather weaker growth, but in leaf-form and method of branching it is identical with that of *B. stricta*, and the author is of the opinion that they are conspecific. Both names are consequently reduced to synonymy and Lessing's combination is confirmed.

Syntype material of *B. Sieberi* (New Holland, 1825, Sieber, No. 485) and *B. Sieberi* var. *Gunnii* ("Van Diemen's Land, Gunn") is at Geneva, but the specimens do not bear mature fruit. De Candolle's description, however, indicates that they were of the "aculeata" form. The above-mentioned specimens were nominated lectotypes of the species and variety respectively, but the names themselves are considered synonymous with *B. aculeata* in that they were applied merely to ecological variants.

B. scapiformis was described by De Candolle at the same time as *B. stricta* and *B. Sieberi*, being separated from these species on purely vegetative characters. No particular specimens are cited in the original description which is followed immediately by that of two varieties; *puberula* ("Smith's plains near Lachlan R., A. Cunningham") and *glabra* ("Van Diemen's Land, Gunn"). Syntype specimens of these two varieties are at Geneva, but only that of the former variety bears fruit and was nominated lectotype ("Smith's Plains, Lachlan River, New South Wales, 25 June, 1817, A. Cunningham").

In the long series of specimens examined, a large number have been satisfactorily matched with one or other of De Candolle's species, but an equally large number occupy an intermediate position. This indicates that no real discontinuities occur between these populations, and that in the past a separate specific epithet was applied to each peak of variation. By recognizing that the term *B. aculeata* covers a widespread population, individuals of which are sometimes strikingly different in habit due to the age of the plant or ecological factors, it is undesirable and fulfils no useful purpose to perpetuate the confusion of terminology arising from the practice of giving each variation distinct status.

Two syntype specimens of *B. cuneifolia* Tate are in the Herbarium of the University of Adelaide, one of which is nominated lectotype. In the original description, Tate records that the fruits bear a "membranous entire wing", but on microscopic examination this is seen to be irregularly indented.

The author has been unable to examine authenticated syntype specimens of *B. leucanthemifolia* Benth., *B. oblongifolia* Benth., and *B. glauca* Walp. These are listed in the above synonymy on Bentham's authority.

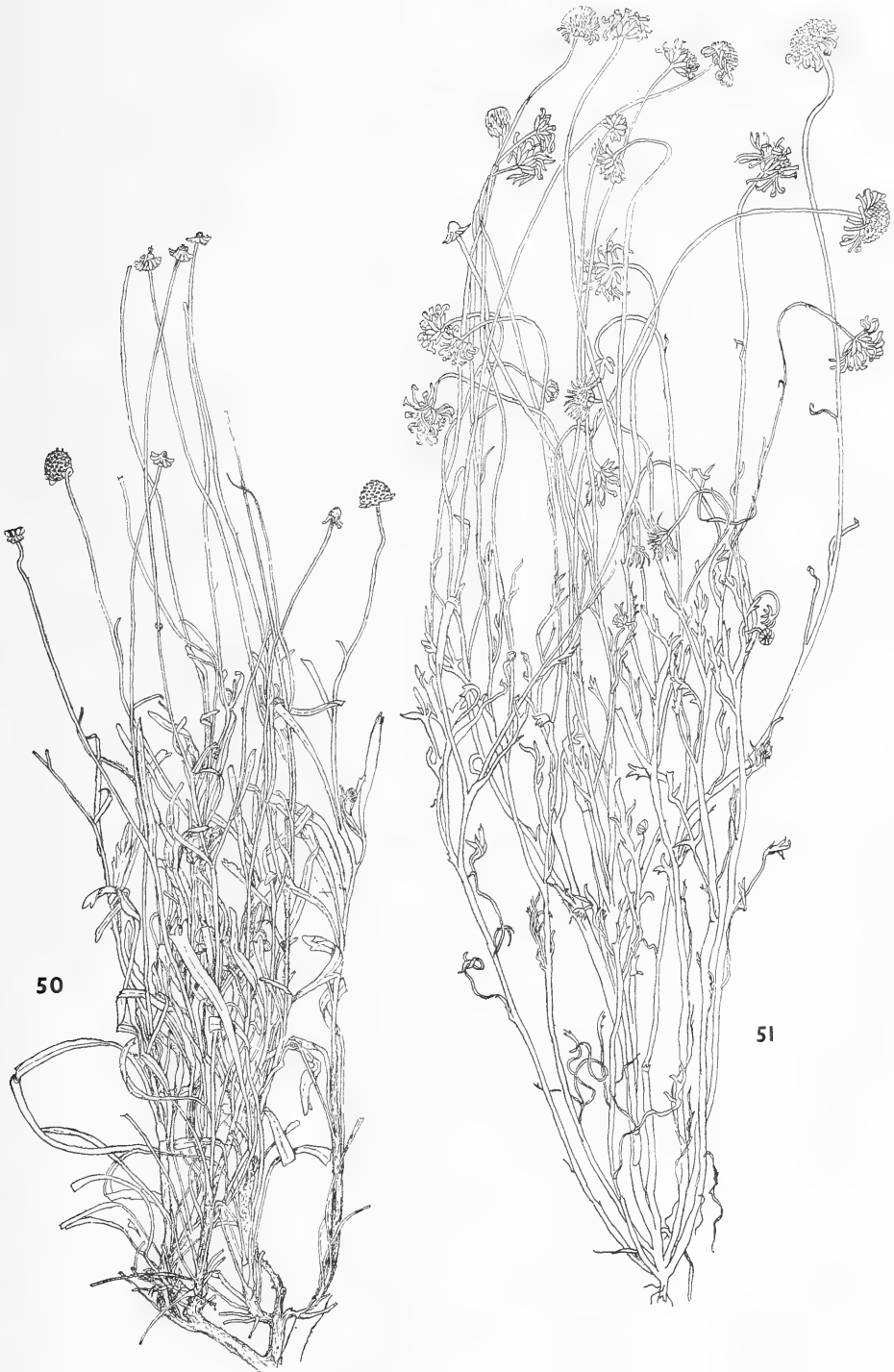
Variation noted in the fruit is little more than is often found within the same capitulum. Usually the wing is macroscopically dissected, but in specimens where it appears to be entire microscopic examination shows it to be shallowly dissected.

The relation of the wing to the body in the fruit of this and the following species of this group shows a marked difference from the condition in the foregoing winged species, in that the two structures are not sharply demarcated. In transverse section, the fruit is roughly elliptical and in many cases the point of junction between wing and body cannot be determined with accuracy.

In its flat non-tuberculate nature, and incompletely dissected wing, *B. aculeata* is apparently the most primitive member of this group, but whether the other species took their origin from it directly or not is debatable.

23. BRACHYCOME MARGINATA Benth., Enum. Pl. Hueg. (1837), 60.

An erect perennial, branching from the base, rarely exceeding 36 cm. in height. Indumentum of woolly hairs confined to the leaf axils or forming a very sparse to dense covering to the whole plant; short glandular hairs sometimes also present to a varying degree. Cauline leaves numerous, up to 8.5 cm. long, 7.5 mm. broad, sessile, usually narrow-cuneate to cuneate with three acute terminal teeth or lobes, sometimes pinnatisect with up to 8 linear segments; occasionally entire, linear to broad-linear or narrow-oblong. Radical leaves only present in young plants, similar in shape and size to the lower cauline leaves of the same plant. *Peduncles* sparsely leafy proximally, more or less glandular-pubescent and woolly. *Capitula* 1-200, up to 1 cm. diameter. *Involucral bracts* 18-23, 3-4.6 mm. long, 1-2.5 mm. broad, narrow-obovate and obtuse, or oblanceolate and acute, serrulate to slightly torn-ciliate, more or less woolly and glandular. *Ray florets* 33-35, the rays white or yellow, seldom mauve, up to 9 mm. long, 2 mm. broad. *Receptacle* 1.5-3.5 mm. broad, 1.3-3.5 mm. high, conical, usually scarcely pitted, occasion-



50

51

Text-figures 50-51. Habit studies. $\times \frac{1}{2}$.
50, *B. marginata* var. *marginata*. 51, *B. papillosa* (holotype).

ally moderately so. *Fruit* 3-4 mm. long, 2.6-3 mm. broad, light brown, broad-cuneate in rough outline, flat, winged; body of fruit elliptical, frequently bearing relatively long tubercles at maturity; wing broad, irregularly and deeply dissected. Pappus conspicuous.

Key to the varieties.

Rays white, rarely bluish var. *a marginata*.
Rays orange-yellow var. *β chrysoglossa*.

Brachycome marginata Benth. var. *a marginata* comb. et stat. nov.

Enum. Pl. Hueg (1837), 60.

(Text-figs. 50, 59; Plate vi, map 18.)

Synonymy: *B. heterodonta* DC., Prod. v (1836), 305. *B. calocarpa* F. Muell., Linnaea xxv (1852), 399.

Type data: ? locality, Ferd. Bauer (syntype material at Kew).

Agrees in all particulars with the general description, the distinctive character being the colour of the rays, which are usually white, though occasionally a specimen is found in which they are bluish.

Habitat: Grassland.

Range: Relatively common in eastern States and south-eastern South Australia.

Specimens examined:

Queensland: Peak Downs, F. Mueller (MEL); Gindee, 8.1916, C. T. White (BRI); Minerva, Leichhardt district, "in open brigalow-bloodwood parkland on black silty clay, cir. 800 ft. Tufted, erect, light green, disc yellow, ray white", 22.7.1934, S. T. Blake (BRI); Burnett R., F. Mueller (MEL); *Mt. Playfair, 1890, Bidduiph (MEL); Morven, "in cemetery enclosure on fairly heavy soil, about 1,400 ft.", 1.5.1934, S. T. Blake (BRI); *Roma, R. Scortechini (BRI); *Plain of the Condamine, Pemberton Hodgson (MEL); Condamine R., F. Mueller (MEL); *Main Range, C. H. Hartman and F. M. Bailey (BRI); Wyreema, 1.749, 17.3.1931, C. E. Hubbard, n. 5889 (BRI); Clifton, 12.1912, C. T. White (BRI, NSW); Silverwood, 7.1922, C. T. White, n. 1748 (NSW); *St. George, 5.1894, J. Wedd (BRI); *Bybera, "clayey soils", 5.9.1935, C. T. White, n. 10752 (BRI); Inglewood, 9.1910, J. L. Boorman (NSW); near Ballandean, 11.1944, M. S. Clemens (BRI); Noondoo, Maranoa District, "in grassland plain, grey, silty clay, about 550 ft.", 4.3.1936, S. T. Blake (BRI); *Warrego district, Joonamurra, "chocolate clay soil", 20.9.1938, S. L. Everist, n. 1676 (BRI); Cooper's Creek (MEL).

New South Wales: Wallangra, 4.1913, J. L. Boorman (NSW); Ashford, 3.1908, E. M. Hazes (NSW); Moree, 7.1905, J. L. Boorman (NSW); *Moree, 16.10.1917, J. B. Cleland (AD); Molroy, near Bingara, 29.10.1938, A. H. Noble (NSW); Glen Innes, 11.1911, F. H. Kenny (BRI); Glen Innes, "among grasses", 3,520 ft., 8.4.1931, C. E. Hubbard (BRI); Jennings, 12.1903, J. H. Maiden and J. L. Boorman (NSW); Howell, "moist pasture land", 1.1906, J. L. Boorman (NSW); Guyra, "commingled with grasses", 6.1917, J. L. Boorman (NSW); Wollomombi, 31.1.1941, "white to mauve", G. L. Davis (NSW); near Hillgrove, 22.2.1941, G. L. Davis (NSW); Armidale, 1871, F. Mueller (NSW); Armidale, "pasture land", 21.2.1941, G. L. Davis (NSW, BRI); Armidale, "roadside", 22.2.1941, P. Voisey (NSW); Armidale, 19.11.1941, Consett Davis (NSW, BRI); Gara R., "grassland", 16.2.1941, G. L. Davis (NSW, BRI, MEL); Dangar's Falls, 4.1941, B. Bassinett (NSW); New England, C. Stuart n. 236 (MEL); Tamworth, 6.1904, J. L. Boorman (NSW); Tamworth, 6.1906, J. H. Maiden and J. L. Boorman (NSW); Moonbi, 20.10.1886, E. Betche (NSW); Scone, 8.1899, J. H. Maiden (NSW); Singleton, 4.1908, J. L. Boorman (NSW); Hunter River, 1802-5, R. Brown (MEL); Sofala, 3.1910, J. H. Maiden and R. H. Cambage (NSW); Bathurst, 9.3.1891, R. T. Baker (BRI); Gulgong, 3.1901, J. H. Maiden and J. L. Boorman (NSW); Euchareena, 6.1900, J. L. Boorman (NSW); Bowan Park, near Cudal, 10.1906, 11.1907, W. F. Blakely (NSW); *Conoblas, 15.10.1916, J. B. Cleland (AD); Lachlan R. (NSW); Rockley, 11.1906, J. L. Boorman (NSW); Jenolan Caves, 10.1899, W. F. Blakely (NSW); Wyalong, 22.9.1906, J. L. Boorman (NSW); Young, 11.1915, J. B. Cleland (AD); *Temora, 9.1915, J. W. Dwyer (NSW); Temora, 11.1917, J. L. Boorman (NSW); *Hay, 9.1889, J. J. Fletcher (NSW); Zara, near Hay, 3.1904, E. Officer (NSW); South Goulburn, 10.1906, J. Lumsden (NSW); Queanbeyan, 1.1888, E. Betche (NSW); *Rules Pt., west of Kiandra, 26.11.1921, A. Forster (NSW); *Cooma, 12.1890, E. Betche (NSW); Cooma, 13.2.1908, R. H. Cambage (NSW); Nimity-belle to Cooma, 12.1896, J. H. Maiden (NSW, *MEL); Bombala, 12.1896, J. H. Maiden (NSW); *Echuca (BRI); Walgett, plain, 9.1942, N. C. W. Beadle (NSW); Burren Junction, 6.1907, J. L. Boorman (NSW); Pilliga, 8.1907, J. L. Boorman (NSW); *Brewarrina, 10.1912 (NSW); Brewarrina, 11.1903, J. L. Boorman (NSW); Coolabah, 10.1900, R. W. Peacock (NSW); Coolabah, 6.1901, J. L. Boorman (NSW); Girilambone, 11.1890, E. Betche (NSW); The Brothers, Girilambone, 3.1900, W. Bauerlen (NSW); Boppy Mt., 7.1903, W. Bauerlen (NSW); Cobar, 3.1910, 8.1911, L. Abrahams (NSW); Warren, "heavy brown soil, treeless plain", 1.1942, N. C. W. Beadle (NSW); Nevertire, 30.9.1886, E. Betche (NSW); *Gilgunnia, 12.1903, W. Bauerlen (NSW); Co. Yantapa,

1941, N. C. W. Beadle (NSW, MEL, BRI); Co. Ularara, 1941, N. C. W. Beadle (NSW, BRI, MEL); *Broken Hill district, 5.1917, J. B. Cleland (AD); Broken Hill, 22.8.1939, J. W. Vickery and I. M. Pidgeon (NSW); Broken Hill, 10.4.21, A. Morris (NSW); Myalla, 26.1.1924, A. Morris (NSW, BRI); Balaclava Swamp, 45 m. east of Broken Hill, 1.4.1917, J. B. Cleland (NSW); Horse Lake, 27.5.1928, A. Morris (BRI); Boxtank, near Menindee, "plain, red loam", 5.1940, N. C. W. Beadle (NSW, MEL, BRI); Darling R., "sandhills", Beckler, Vict. Expl. Exped. (MEL, NSW); Darling R., ? F. Mueller (MEL); Wentworth, 10.94, R. T. Baker (NSW); Wentworth, Leichhardt (MEL); Cal Lal, 40 miles W. of Wentworth, 20.8.1946, J. Vickery (NSW).

Victoria: Murray River, Dallachy (MEL); Murray R., F. Mueller (MEL); *Murray R., Blandowski (MEL); Wimmera, "plains", Dallachy (MEL); Charlton, 10.1917, W. W. Watts (NSW); Shire of Borung, "open woods", 27.9.1903, F. M. Reader (MEL); Borung, 11.1921, D. J. Paton (MEL); Nhill, 4.1911, J. Staer (NSW); *Nhill, St. Eloy D'Alton (MEL); Dimboola 11.10.1891, F. M. Reader (MEL); Dimboola, 1903, St. Eloy D'Alton (NSW); *Grampians, 11.1900, C. Walter (NSW); Wickliffe, 11.1903, H. B. Williamson (MEL, NSW, BRI); Bacchus Marsh, 11.1853, F. Mueller (MEL); Bacchus Marsh, 3.11.1910, J. R. Tovey (MEL); Melton, 4.1911, J. Staer (NSW); Rockbank, 4.1911, J. Staer (NSW); St. Albans, "basalt plains", 7.6.1900, P. R. H. St. John (MEL); Altona, "basalt plains", 23.10.1903 (MEL); Little River, F. Mueller (MEL); Little R., "basalt plains", 1.11.1904, P. R. H. St. John (MEL); Little R., 11.1903, Fullager (NSW); Skipton, "plains", Whan (MEL); Geelong, 11.1909, 1913, H. B. Williamson (MEL); Black Forest, 12.1852, F. Mueller (MEL); Williams River, 1802-5, R. Brown (MEL); Comet River, B. Aibsham (MEL).

South Australia: Mt. Lyndhurst, 9.1898, 8.1899, M. Koch (AD); Hawker, 19.10.17, J. M. Black (JMB); Eurelia, C. A. Brown (JMB); Paringa, 1.1884 (AD); *Loxton, 21.8.24, J. B. Cleland (CL); *Kapunda, R. Tate (AD); Tanunda, 2.1847, F. Mueller (MEL); Mannum, 23.5.1880, *5.3.1883, R. Tate (AD); 13.4.24, J. B. Cleland (JBC); Murray, "Mallee Scrub", F. Mueller (MEL); Lameroo, 10.10.1918, J. M. Black (JMB, MEL); Cudnaka, 10.1851, F. Mueller (lectotype, *B. calocarpa*, MEL; lectoparatype, NSW).

This species is very variable in vegetative characters and has presented considerable difficulty in defining its limits. In the original description, and subsequently in Fl. Aust. (1866) Bentham states, "quite glabrous", and this has always been accepted as being the case, the densely woolly specimens being relegated to *B. calocarpa*. However, examination of a long series of specimens has failed to reveal a single one to which the term "glabrous" can correctly be applied. The author is indebted to Mr. J. S. L. Gilmour of the Royal Botanic Gardens, Kew, for the following information: "The type specimen of *B. marginata* Benth. is almost glabrous except for a few scattered while rather stiff hairs. I would scarcely call them woolly in the ordinary sense of the term, and they are very few and far between". Unfortunately no syntype material of this species is available in Australia, but two specimens have been examined which were quoted by Bentham in Fl. Aust. under *B. marginata*. Presumably he was satisfied that the specimens were conspecific with the type, but careful examination shows that they are both sparsely woolly. The difference between *B. calocarpa* and *B. marginata* being merely one of degree, not of nature, the only logical course is to abandon the former name and redescribe *B. marginata* in a broader sense.

Bentham himself, apparently, had some doubts as to the status of these species as in Fl. Aust. he remarks, in connection with *B. calocarpa*, "the species appears to differ from *B. marginata* chiefly in the colour of the ray; the notes, however, of collectors are in this respect somewhat vague, and it is possible that the two may be varieties only". His observation as to the colour of the ray is explained by the fact that he reduces *B. chrysoglossa* to a synonym of *B. marginata*. In the original description of *B. marginata*, the colour of the ray is not mentioned, so this action implies that all members of *B. marginata* have yellow rays. His implication, however, cannot be taken seriously, as there is no means of determining from herbarium specimens the natural colour of the rays, and that of the type specimen must always remain in doubt. To confuse the matter further, it has been found in plants transplanted and kept under observation, that when first expanded the rays are frequently sulphur-yellow, becoming white after a maximum of two days. It is not uncommon to find plants bearing both white and yellow flowers simultaneously, the latter being recently expanded.

Syntype specimens of *B. heterodonta* DC. are in the De Candolle herbarium, Geneva, and the author is indebted to Professor C. Baehni for sending fruit and florets from them for examination. These are identical with those of *B. marginata*, and photographs

of the actual specimens confirm this resemblance. The specimens in question bear Alan Cunningham's original labels, and are from two localities, "wet plains on the Lachlan R., interior of New South Wales, 10 May, 1817", and "swampy ground, Sidmouth Valley, near Bathurst, New South Wales, April, 1817", the latter being nominated lectotype though the name itself is reduced to synonymy.

The fruits of this species are relatively constant in character, variation being confined to the number of segments into which the wing is dissected. As differences of this nature are noted between fruits on the same capitulum, this variation has no diagnostic importance. Considerable variation has been observed in the degree of development of the tubercles, the size of which depends very largely on the degree of maturity of the fruit. Even in quite advanced fruits the presence of the tubercles may be merely indicated by slight swellings, each bearing a single glandular hair, while on the same plant there may be fully mature fruits with dense finger-like tubercles. However, their presence at maturity is by no means invariable, and it has been found that there is a rough correlation between the degree of development of the tubercles, and the indumentum. In those plants which are densely woolly-white, the tubercles are large enough to be seen macroscopically, whereas those in which the woolliness is confined to the leaf axils or is very sparse, bear fruits on which the tubercles are small or only represented by curled hairs. All intermediate conditions are found so that it has not been possible to base a dichotomy in the species on these characters.

Although the leaves are typically narrow-cuneate with three distal teeth, cases are not uncommon in which the lower ones are pinnatisect. When this occurs the segments are usually confined to the distal half of the leaf, but specimens have been seen from Moree, Broken Hill district and Condamine R., in which they are confined to the proximal portion. In each case, however, the upper leaves are typical.

Attempts to correlate the density of indumentum with geographical position has been inconclusive. It has been noted, however, that the majority of the conspicuously woolly specimens have been collected from western districts, and the sparsely woolly ones from localities nearer the coast. There are numerous instances in which both types occur in the same locality, though the sparsely woolly forms are the most common in Queensland and on the northern tablelands of New South Wales. As a group, the specimens from New England have a closer glandular pubescence and less woolliness than those from other localities, and the tubercles on the fruit are less well defined.

The similarity between the fruits of *B. marginata* and those of *B. aculeata* should be noted, particularly as there is sometimes a certain amount of vegetative resemblance. They are, however, readily distinguished by the fact that in *B. marginata* the wing is completely dissected and is much broader in proportion to the breadth of the body. Woolly hairs are never found on the stems of *B. aculeata*. It is obvious that both these species are closely related, *B. marginata* having probably originated directly from *B. aculeata* or its immediate ancestral form.

Brachycome marginata Benth. var. β *chrysoglossa* (F. Muell.) comb. nov.

(Plate vi, map 18.)

Synonymy: *B. chrysoglossa* F. Muell., Trans. Phil. Soc. Vic., i (1855), 44.

Lectotype: Murray River, 1853, F. Mueller (MEL).

Lectoparatype: l.c. (MEL).

Ray florets brilliantly orange-yellow, otherwise identical with var. *marginata*.

Habitat: Grassland.

Range: New England Tableland and north-western Victoria.

Specimens examined:

New South Wales: River Severn, New England, C. Stuart, n. 174 (MEL); Armidale, 1871, Perrott, n. 93 (MEL); Armidale, "open forest", 20.1.1941, G. L. Davis (NSW, MEL, BRI); Pine Forest, near Armidale, 22.12.1940, 20.11.1941, G. L. Davis (NSW, MEL, BRI); New England, C. Stuart, n. 174 (MEL).

Victoria: Murray River, 1853, F. Mueller (lectotype, lectoparatype of *B. chrysoglossa*, MEL); Murray R., 11.1905, C. French, Jnr. (MEL); Murray Scrub, 1850, F. Mueller (MEL); Sea Lake, 9.1917, W. W. Watts (NSW); *Lake Hindmarsh (MEL); Horsham, St. Eloy D'Alton (MEL); *Katyil, near Dimboola, "roadsides", 31.5.1896, F. M. Reader (MEL).

This variety was given specific status by Mueller, and it is recognized that the distinctive colour of the ray florets, unique in this genus, merits separate status. In view of the fact that in other respects specimens are identical with those of *B. marginata*, it is considered desirable to include it under that species with varietal rank. Unfortunately specimens cannot be identified with certainty in the dried condition, unless they are accompanied by collector's notes indicating the natural colour of the rays. Even when such information is supplied it may be unreliable if the colour is merely described as yellow. In the case of the specimen from Comet R., the collector records that both yellow and white flowers occur on the same plant. This is clearly a specimen of *B. marginata* var. *marginata*, in which, as noted above, the rays are commonly sulphur-yellow when first expanded, later becoming white. In the list of specimens cited, the only ones for which the author can vouch are those collected personally. The remainder have been identified as *B. chrysoglossa* at the various herbaria to which they belong and it is assumed that determination was based on information not recorded with the specimens. In each specimen the rays are of such a colour as to indicate they may have been yellow originally. It is expected that some, at least, of these specimens belong to var. *marginata*, but attempts to link up the colour of the rays with some more permanent morphological character having failed, an accurate estimation of the range of this variety must await more careful collecting.

It has been noted in plants from the Armidale district that local populations of both varieties are identical except for the colour of the rays, though in no instance have they been found intermixed.

Variation is similar to that recorded for var. *marginata*, from which it would appear that var. *chrysoglossa* took its origin in quite recent times. No specimens have so far been seen in which the body bears long tubercles or are densely woolly, but the series is too short to justify any generalizations on that score.

24. BRACHYCOME PAPILLOSA, SP. NOV.

(Text-figs. 51, 60; Plate vi, map 19.)

Holotype: Near Mossgiel, N.S.W., "saltbush plain, grey clay loam", 8.1942, N. C. W. Beadle (NSW).

Herba perennis, erecta, ramosissima, ad 36 cm. alta, glanduloso et septato pilosa, ramosis junioribus albo tomento. Folia caulina sessilia ad 7 cm. longa, integra aut pinnatifortita-pinnatisecta, lobis circiter 8 acutis ad 7 mm. longis, 2 mm. latis. *Pedunculi* basi foliosi. *Capitula* ad 27, transverse lata 6-11 mm. *Involucri phylla* circiter 18, 3.2-5.5 mm. longa, 1.1-1.5 mm. lata, angusto-oblonga-elliptica, acuminata, glanduloso et septato-pilosa, margine fimbriato-ciliata. *Flores radii* ad 42, ligulis 8 mm. longis, 1.2 mm. latis, verisimiliter violaceis. *Receptaculum* 2.4-4 mm. latum, 2.5 mm. altum, hemisphaericum, satis punctatum. *Achaenium* 2.8-3.5 mm. longum, 2-3 mm. latum, late obovatum, oblongum, fulvum; corpus oblongo-cuneatum, papillis utriusque densis, compressis; alae fere tam latae quam corpus, margine integro aut undato. Pappus conspicuus incisura intra alas tam longum aut fere tam longus.

Erect many-stemmed perennials (?) up to 36 cm. high, glandular- and septate-hairy, the young branches more or less woolly white. Leaves cauline, sessile, up to 7 cm. long, entire or pinnatifortite to pinnatisect, with about 8 acute lobes up to 7 mm. long, 2 mm. broad. *Peduncles* leafy proximally. *Capitula* up to 27, 6-11 mm. diameter. *Involucral bracts* about 18, 3.2-4.5 mm. long, 1.1-1.5 mm. broad, narrow-oblong to elliptical, acute, glandular- and septate-hairy, with torn glandular-ciliate margins. *Ray florets* up to 42, the rays 8 mm. long, 1.2 mm. broad, apparently mauve. *Receptacle* 2.4-4 mm. broad, 2.5 mm. high, hemispherical, moderately pitted. *Fruit* 2.8-3.5 mm. long, 2-3 mm. broad, broadly obovate to oblong, golden-brown; body oblong-cuneate, with dense flattened papillae on each face; wings almost as broad as the body, with an entire or undulating margin. Pappus conspicuous, equal to the notch between the wings or almost so.

Range: South-western districts of N.S.W.,

Specimens examined:

New South Wales: Mossgiel, "saltbush plain, grey clay loam", 8.1942, N. C. W. Beadle (holotype, NSW); Wanganella, 6.1903, 12.1904, E. Officer (NSW); Urana, 11.1924, Flock (NSW).

This species is known from only three localities, but the characters of the fruits warrant specific status, in that the eminences on the body instead of being tuberculate, are flat and almost foliaceous. The series being so short, comments on variation are premature, but in vegetative features the *Mossgiel* and *Urana* specimens seem to represent extremes of specific limits, and it remains to be seen whether intermediate forms are found. The fruits of both specimens are almost identical, though it is noted that in the one from *Urana* the wings have a somewhat frilled appearance, whereas they are flat in the holotype. The *Wanganella* specimens are very similar to the holotype in the possession of pinnatisect leaves, but the plant itself is more robust and less woolly, though not as sparsely so as in the *Urana* specimen.

This species appears to be localized in its distribution, and to have originated from an ancestor of the *B. marginata* type, with which species there is close vegetative similarity. The fruit, however, shows a specialization of the tubercles, and the entire wing, though usually a primitive character, is in this case thought to be secondarily acquired.

25. BRACHYCOME CURVICARPA SP. NOV.

(Text-figs. 52, 61, Plate vi, map 19.)

Holotype: Near Walgett, "Coolabah savannah, dark grey self-mulching soil", 9.1942, N. C. W. Beadle (NSW).

Herba annua, erecta aut adscendens, ramosissima, ad 41 cm. alta, glandulosa, tomento in caulibus foliisque raro-denso. Folia caulina sessilia, ad 5 cm. longa, lobis plerumque ad apicem, ad 4 mm. longis, 1.5 mm. latis, subacuminatis-acuminatis pinnatipartita, raro integra. Folia radicalia caulini inferioribus similia in parvis herbis solum adsunt. *Pedunculū* vel in apice tomentosi vel in basi glandulosi foliosi. *Capitula* ad 60 transverse lata 1.2 cm. *Involucri phylla* circiter 22, 4-4.2 mm. longa, 1.3-1.6 mm. lata, oblanceolata, subacuminata-acuminata, septato-pilosa, mic. serrata. *Flores radii*, circiter 34, ligulis 6-13 mm. longis, 0.5-1.7 mm. latis vel albis vel violaceis. *Receptaculum* 2.8-4.5 mm. latum, 2.4-3.7 mm. altum, hemisphaericum, vix punctum. *Achaenia* 2 mm. longa, 1.2 mm. lata, obovata, alata, firme flexa, fusca-ex fusco subnigra; corpus pilis brevibus glandulosis; alae tenues, quadruplo longiores quam corporis latitudo, implicate praeter margines glanduloso-pilosae, vel integrae vel tenuiter dentosae. Pappus conspicuus.

Erect or ascending many stemmed branching (?) annuals up to 41 cm. high, glandular and sparsely to densely woolly on stems and leaves. Leaves cauline, sessile, up to 5 cm. long, pinnatipartite with mainly distal segments up to 4 mm. long, 1.5 mm. broad, sub-acute to acute, rarely entire. Radical leaves present only on young plants, similar to the lower cauline leaves. *Peduncles* either woolly-white distally or glandular, leafy proximally. *Capitula* up to about 60, 1.2 cm. diameter. *Involucral bracts* about 22, 4-4.2 mm. long, 1.3-1.6 mm. broad, oblanceolate, sub-acute to acute, septate-hairy, microscopically serrulate. *Ray florets* about 34, the rays 6-13 mm. long, 0.5-1.7 mm. broad, white or lavender. *Receptacle* 2.8-4.5 mm. broad, 2.4-3.7 mm. high, hemispherical, hardly pitted. *Fruit* 2 mm. long, 1.2 mm. broad, obovate, winged, strongly curved, medium to very dark brown; the body bearing short glandular hairs; wings thin, about four times the breadth of the body, infolded and glandular hairy along the edge, entire or shallowly incised. Pappus conspicuous, white.

Range: Queensland, through western New South Wales to western Victoria. Canal Creek (Q.) is the only record from a coastal locality.

Specimens examined:

Queensland: Canal Crk., C. Hartmann (BRI); *Longreach, 10.1913, E. Jarves (BRI); west of Winton, Gregory North District, "in channels of Western R.", "low bushy subglaucous annual with yellow flowers", 28.10.1935, S. T. Blake (BRI); Duneira, 12 miles S.E. of Blackall, "small tufted herb with erect flowering stalks in brown clay soil, with *Astrebla lappacea*", 27.9.1939, S. L. Everist, n. 1853 (BRI); Mineeda, 7 miles E. of Blackall, "small herb on grey clay soil carrying *Astrebla lappacea*, rays mauve", 18.7.1939, S. L. Everist, n. 1849 (BRI); Mineeda, "small erect or obliquely ascending herb on open downs country, chocolate soil. Florets very pale lavender", 25.8.1935, S. L. Everist, n. 1246 (BRI); near Blackall, 8.1928, W. MacGillivray (BRI); Mount Howitt Station, Gregory South District, "in open plain, grey silty clay. Stem solitary or tufted, erect to 1 ft. Leaves slightly olive green. Ray white, disc yellow", 6.7.1936, S. T. Blake (BRI);

Bungunya, Darling Downs, "in *Astrebala elymoides* grassland, 600 ft., erect pale green tufts. Ray white, disc yellow", 17.7.1945, S. T. Blake (BRI); Yelarbon, "in more or less open places on light grey sand, 800 ft. Tufted, erect, deep green, (?) perennial. Flowers rich yellow", 22.2.1936, S. T. Blake (BRI).

New South Wales: Bokkara Ck., 22.10.1846, L. Leichhardt (MEL); Boggabilla, "on sandy soil in rung forest, common", 1.1935, C. W. Winders (BRI); Gravesend, 5.1914, W. M. Carne (NSW); Warialda, 7.1905, H. M. R. Rupp (NSW); Warialda, 10.1914, J. L. Boorman (NSW); Narrabri, 11.1899, J. H. Maiden (NSW); Narrabri, 8.1907, J. L. Boorman (NSW); Narrabri, 9.1913, E. Breakwell (NSW); Boggabri, 10.1912, R. H. Cambage (NSW); Chilcott's Creek, near Warrah, 10.1897, J. Gregson (NSW); near Walgett, "Coolabah savannah, dark grey self-mulching soil", 9.1942, N. C. W. Beadle (holotype, NSW); 20 miles east of Walgett, "under trees of *E. Coolabah*, dark grey, self-mulching clay loam", 6.1943, N. C. W. Beadle (NSW, MEL); Bourke, 8.1896, J. H. Maiden (NSW); Coonamble, 4.1913, W. H. Potts (NSW); The Brothers, Girilambone, 3.1900, W. Bauerlen (NSW); Nyngan, 3.1904, J. H. Maiden and J. L. Boorman (NSW); Nevertire, 30.9.1886, E. Betche (NSW); Trangie, 10.1911, L. Abrahams (NSW); Trangie, 9.1916, E. Larcombe (NSW); Trangie, 16.10.1924, A. Morris (NSW); Govt. N.W. Expedition, 1903, H. Basedow (NSW); Wilcannia, 20.8.1939, J. W. Vickery and I. M. Pidgeon (NSW); Til Til, Co. Kilfera, "Saltbush plain, grey clay loam", 8.1942, N. C. W. Beadle (NSW); Wanganella, 6.1903, E. Officer (NSW); Jerilderie, 10.1920, Dwyer (NSW).

Victoria: Yarriambiack Crk., Shire of Borung, 9.9.1903, F. M. Reader (MEL).

The outstanding characteristics of this species are the possession of curved fruit and a strong tendency towards infolding of the wings. A certain amount of variation is apparent in the degree of infolding, in some it being relatively slight while in others the edge of the wing is recurved almost to the body. In all cases, however, the curvature of the fruit is more than could be accounted for by lateral pressure in the head.

Vegetative variation is not unduly great in this reasonably long series from a large area. A specimen from Tamworth (11.1904, H. M. R. Rupp, NSW) has been examined in which the lower leaves are narrow-cuneate and apically toothed, and the flowers are abnormally large, being up to 1 cm. in diameter, excluding the rays. Unfortunately the fruits are not quite mature, but appear to be curved. This specimen has not been cited in the list of those examined, because of the strong vegetative resemblance to *B. aculeata* and the absence of fully mature fruit.

If the fruits of this species were flattened out, there would be little to separate them from those of *B. aculeata*. For this reason it is considered that *B. curvicarpa* originated directly from that species rather than from *B. marginata*, with which it agrees in the presence of woolly hairs on the stems.

26. BRACHYCOMA MUELLERI Sond., *Linnaea* xxv (1852), 475.

(Text-figs. 53, 62, 63; Plate vi, map 20.)

Haptotype: Para River, "grassy plain", 9.1851, F. Mueller (MEL).

A glabrous (?) annual up to 20.5 cm. high, branching from the base, leaves cauline, stem-clasping, up to 12 cm. long, irregularly pinnatifid; segments ovate, mucronate, up to 1.1 cm. long, 4 mm. broad, the distal segments frequently lobed again. *Peduncles* robust, bearing 1-3 linear, entire, bract-like leaves. *Capitula* up to 20, 1 cm. diameter. *Involucral bracts* 14-16, 4-5.5 mm. long, 1.4-2 mm. broad, oblanceolate, acute, entire with a row of microscopic glandular hairs around the margins. *Ray florets* 28, the rays about 5 mm. long, 0.7 mm. broad. *Receptacle* 2 mm. broad, 1 mm. high, convex, slightly pitted. *Fruit* 2 mm. long, 1.5 mm. broad, black; body terete and striate, in one aspect being partially enclosed by the two lateral entire wings which fold back on themselves. Pappus a ring of very minute teeth.

Range: Gawler and Iron Knob districts.

Specimens examined:

South Australia: Cooroona, Iron Knob, 6.1885, W. L. Cleland (JBC, JMB); Para River, 9.1851, F. Mueller (haptotype, MEL); near Gawler Town, F. Mueller (MEL).

Attempts to trace syntype material of this species being unsuccessful, a haptotype was selected, which will become the neotype if it is later established that Sonder's specimens are no longer extant. It seems probable that the haptotype represents a duplicate specimen retained by Mueller when he forwarded the other specimens to

Text-figures 52-57. Habit studies. $\times \frac{1}{3}$.

- 52, *B. curvicarpa*. 53, *B. Muellerei* (haptotype). 54, *B. Muelleroides* (holotype).
 55, *B. cardiocarpa* (paratype). 56, *B. nivalis* var. *nivalis* (lectotype).
 57, *B. nivalis* var. *alpina* (lectotype).

Sonder. In the original description Sonder states, "fruits cylindrical, striate, furnished on both sides with a slender glabrous entire wing a little broader than themselves; Pappus very minute". From this it is apparent that the recurved nature of the wing escaped him, and that he did not examine the fruit with sufficiently high magnification to show the extraordinary wing structure.

The development of this type of fruit is foreshadowed in *B. curvicarpa* in which the wing in a number of fruits is slightly infolded. It never, however, reaches the extreme condition seen in *B. Muellerei* where the body is partially enclosed.

27. BRACHYCOME MUELLEROIDES sp. nov.

(Text-figs. 54, 64, 65; Plate vi, map 20.)

Holotype: Wagga, 10.1889, J. J. Fletcher (NSW).

Paratypes: Five, l.c. (NSW, MEL).

Herba annua, infirme erecta aut adscendens, glabra, ad 13.5 cm. alta. Folia caulina, caulem amplectentia, anguste-linearia-linearia, nunc integra nunc 1-2 lobis in inferiore dimidio filiformibus, acuminata, ad 5.5 cm. longa, 1.1 mm. lata. *Pedunculi* filiformes, nudi. *Capitula* 2-21 transverse lata 4 mm. *Involucris* *phylla* circiter 12, 2 mm. longa, 1.2 mm. lata, glabra, ovato-elliptica, obtusa, marginibus mic. glanduloso-ciliatis. *Flores radii* circiter 57 ligulis 2.4 mm. longis, 0.5 mm. latis. *Receptaculum* 2.5-2.7 mm. latum,

1.5–2.3 mm. altum, maxime conicum, vix punctatum. *Achaenia* 0.9 mm. longa, 0.6 mm. lata, obovata, ex fusco subnigra; corpus lineare transverse quadrangulum; alae replicatae fere corporis anteriorem partem continent. Pappus albus circiter quattuor quintis brevior achaenii longitudine.

Weakly erect or ascending glabrous annuals, up to 13.5 cm. high. Leaves cauline, stem-clasping, narrow-linear to linear, entire or with 1 to 2 filiform lobes on the proximal half, acute, up to 5.5 cm. long, 1 mm. broad. *Peduncles* filiform, naked. *Capitula* 2–21, 4 mm. diam., *Involucral bracts* about 12, 2 mm. long, 1.2 mm. broad, glabrous, ovoid-elliptical, obtuse, with microscopically glandular-ciliate margins. *Ray florets* about 57, the rays 2.4 mm. long, 0.5 mm. broad. *Receptacle* 2.5–2.7 mm. broad, 1.5–2.3 mm. high, steeply conical, hardly pitted. *Fruit* 0.9 mm. long, 0.6 mm. broad, obovoid, dark brown; body linear, quadrangular in cross section; wings folded back on themselves, coming almost to enclose the inner side of the body. Pappus white, about one-fifth the length of the fruit.

Range: Riverina district and northern central Victoria.

Specimens examined:

New South Wales: Wagga, 10.1889, J. J. Fletcher (holotype and 4 paratypes N.S.W.; 1 paratype MEL).

Victoria: Nathalia, 10.1930, J. H. Willis (MEL).

This very distinct species is known from only two localities, but further collecting, particularly in intermediate districts, will probably produce further specimens. Unfortunately no ecological notes are available, but the appearance of the specimens suggests that they grew in a damp situation among herbage. All those examined are of a delicate, rather grass-like appearance, so that they would easily be overlooked among taller grasses.

The fruit of this species is a miniature replica of that of *B. Muelleri*, both showing the unique folding of the wings, which lends a somewhat inflated appearance to the fruit itself. The marked difference in actual size of the fruit and relative size of the pappus, together with vegetative features, justifies specific rather than varietal status.

There can be no doubt that both *B. Muelleri* and *B. Muelleroides* are closely related, and it is probable that they both originated from an ancestor of the *B. curvicarpa* type.

28. BRACHYCOME CARDIOCARPA F. Muell. ex Benth. Fl. Aust., iii (1866), 517.

(Text-figs. 55, 66; Plate vi, map 21.)

Synonymy: *B. linearifolia* Hook. f., Fl. Tasm., i (1860), 185.

Lectotype: South Esk, Tasmania, 10.12.(?)1849, C. Stuart (MEL).

Lectoparatypes: l.c. (MEL).

Erect glabrous perennials, up to 42.5 cm. high. Leaves mainly radical, up to 22 cm. long, 0.9–2.2 mm. broad, linear, grass-like, entire, obtuse, the bases concealed by the dead remains of former leaves. Scapes usually robust, leafy proximally. *Capitula* 1–3, 0.8–1.5 cm. diameter. *Involucral bracts* 24–37 in 3–4 rows, 4–6 mm. long, 0.8–2.2 mm. broad, obtuse to sub-acute, narrow-oblong, minutely glandular-pubescent on the outer surface. Outer bracts usually narrower than the inner. *Ray florets* 30–53, the rays 7–10 mm. long, 1.5–2.2 mm. broad. *Receptacle* up to 5.5 mm. high, 4 mm. broad, moderately pitted. *Fruit* 2.1–2.9 mm. long, 1.4–1.8 mm. broad, brown, flat; central body elliptical; wings entire, undulating or irregularly dissected, bearing a few minute glandular hairs marginally. Pappus of moderate size.

Habitat: Marshy ground.

Range: Southern highlands of New South Wales, Port Phillip district of Victoria westward to south-eastern South Australia; central and eastern Tasmania.

Specimens examined:

New South Wales: Quartzville, 11.1900, W. Forsyth (NSW).

Victoria: Warburton, 4.10.1925, A. Morris (NSW); *Ringwood, 4.1910, J. Staer (NSW); *Beaconsfield, 8.1914, A. B. Rendle (MEL); *swamps towards St. Kilda, 9.1852, F. Mueller (MEL); *near Melbourne, 30.9.1883, F. M. Reader (NSW); Melbourne, 9.1898 (NSW); Melbourne, 9.1899, J. H. Maiden (NSW); between Plenty River and Darebin Creek, 10.1852, F. Mueller (MEL); Darebin Creek, 10.1852, F. Mueller (MEL); Hawkesdale, 11.1901, H. B. Williamson (NSW); *Hawkesdale, 11.1904, H. B. Williamson (MEL, BRI); *Portland, W. Allitt (MEL); *Wando Vale, "marsh land", 6.7.1842, J. G. Robert-

son (NSW); Wando Vale, "wet land", 1.8.1842, J. G. Robertson (NSW); Hall's Gap, Grampians, "wild flower garden", 10.1923, C. D'Alton (MEL); Co. Follett, "heaths and pastures", 24.9.1915, F. M. Reader (MEL).

South Australia: *Yallum, R. Tate, n. 18 (AD); *Rivoli Bay, 10.1848, F. Mueller (MEL); Cape Northumberland, lagoon, 16.11.1882, R. Tate (AD); Port MacDonnell, 30.10.1941, J. B. Cleland (JBC).

Tasmania: *Georgetown, 22.11.1842, Gunn, n. 158 (NSW); *Perth, "swamps", 12.1849, C. Stuart (MEL); South Esk, 12.12.1849, C. Stuart (lectotype, lectoparatypes, MEL); Marlborough, 4.1.1841, Gunn, n. 158 (NSW); Formosa, "marshes", 6.11.1843, Gunn, n. 158 (lectotype of *B. linearifolia* Hook. f.); *Cressy, "damp meadow", 20.11.1943, W. N. Curtis (HO); *near Ben Lomond, marsh, R. A. Black (RAB); George's Bay, 9.1892 (NSW); George's Bay, 10.1892, L. Rodway (HO); George's Bay, R. Tate (AD); Harfort, "swamp lands", 25', 29.9.1932, H. J. Hamilton (HO); *Van Diemen's Land, C. Stuart (MEL); Tasmania, 1833, n. 158 (NSW); Tasmania, W. H. Archer (NSW).

When Hooker described *B. linearifolia*, he considered he was merely redescribing De Candolle's species of that name and headed his description "*Brachycome linearifolia* DC., Prodr. v, 306". This was later established by Mueller to be a distinct species and Hooker's specific name being already occupied, it was redescribed as *B. cardiocarpa*, *B. linearifolia* Hook. f. being listed as a synonym (Fl. Aust., iii (1866), 516).

A specimen quoted by Hooker (Formosa, 6.11.1843, Gunn, n. 158) was selected as lectotype of *B. linearifolia*, but in the absence of any direct evidence that this specimen is a syntype also of *B. cardiocarpa*, specimens annotated by Mueller (South Esk River, 10.12.1849, C. Stuart) were nominated lectotype and lectoparatype of the latter species.

B. cardiocarpa var. *alpina* F. Muell. ex Benth. has been relegated to *B. nivalis* F. Muell., the fruit being identical in every way, and at the same time showing certain distinct differences from those of *B. cardiocarpa*.

Vegetative features show no variation except in size, and reliable diagnosis can be made in the absence of fruit and flowers. Although the fruits are constant in general features, some variation was noted in details of the wing, which may be entire or more or less shallowly and irregularly dissected. In no case were glandular hairs seen on the body, which is constantly elliptical in outline.

29. BRACHYCOME NIVALIS F. Muell., Trans. Phil. Soc. Vic., i (1855), 43.

An erect perennial up to 31 cm. high, glabrous except for a sparse glandular pubescence on the petioles and proximal portions of the scapes. Leaves mainly in a radical cluster, broad linear to narrow spatulate, entire to irregularly pinnatifid, up to 8.8 cm. long, or doubly pinnatisect and up to 15 cm. long, including the petiole. Scapes robust, more or less leafy. Capitula 1-3, 1-1.6 mm. diameter. Involucral bracts 25-40, 4.5-8 mm. long, 1-2.6 mm. broad, often in three rows, narrow-oblong to oblong-lanceolate, obtuse to sub-acute, with torn-ciliate margins. Ray florets 30-50, the rays 0.9-1.1 cm. long, 1-3 mm. broad. Receptacle 2.5-3 mm. high, 1.3 mm. broad, convex to conical, moderately pitted. Fruit 2-3 mm. long, 1-2.5 mm. broad, flat, brown, oblong-cuneate in broad outline; body more or less rectangular and well defined, slightly depressed in the central line with a row of glandular hairs; wing entire or shortly lobed, narrow towards the base with minute glandular hairs marginally. Pappus conspicuous.

Key to the varieties.

Leaves doubly pinnatisect var. *a nivalis*
 Leaves entire or irregularly pinnatifid var. *β alpina*

Brachycome nivalis F. Muell. var. *a nivalis* comb. et stat. nov.

(Text-figs. 56, 67, Plate vi, map 21.)

Lectotype: Alpine summits of the Cobbaras Mts., F. Mueller (MEL).

Leaf segments up to 1 cm. long, the distal ones pinnatifid or pinnatisect, with linear, entire or toothed lobes 1.5-4 mm. long, 1 mm. broad, subacute to acute. Leaves on scapes usually entire, sometimes pinnatisect, up to 4.5 cm. long.

Range: Southern Australian Alps at high elevations.

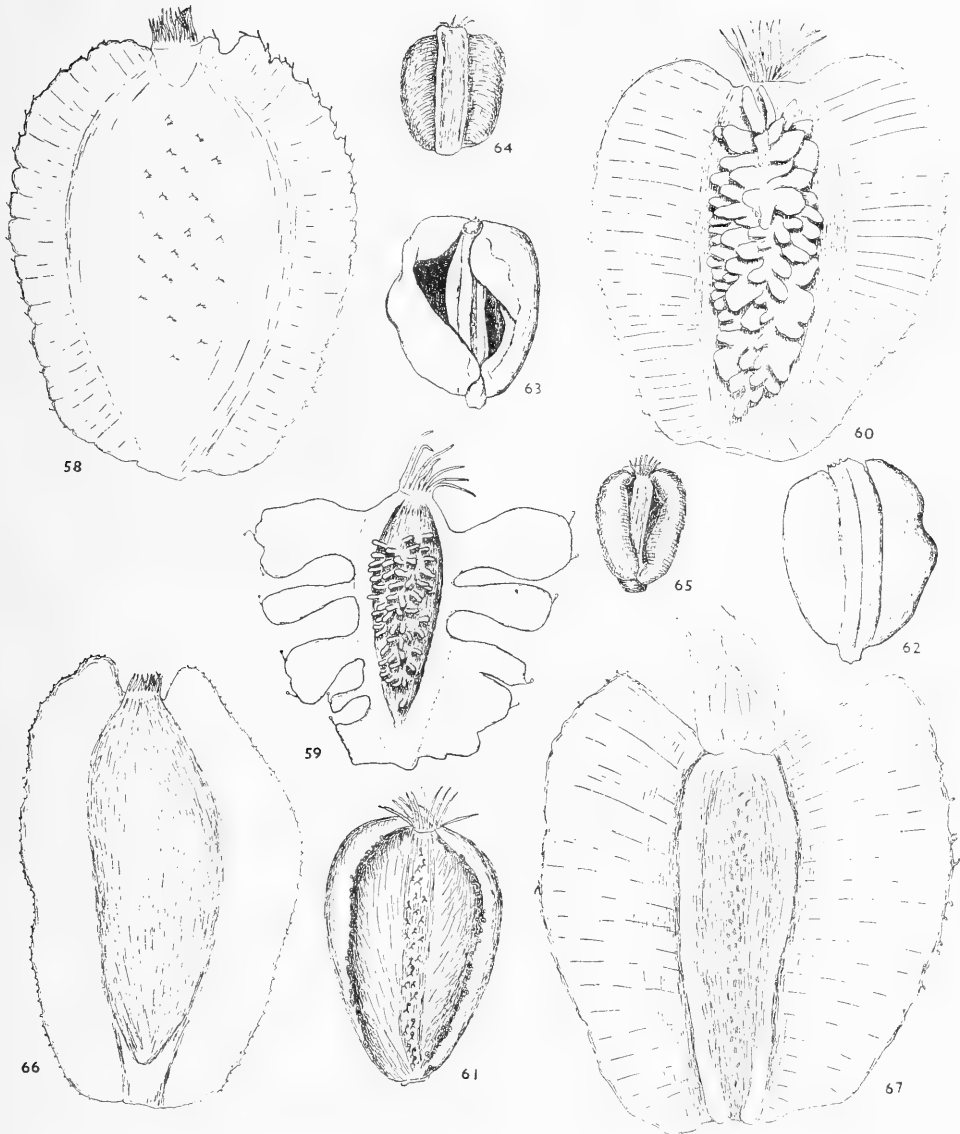
Specimens examined:

New South Wales: Kiandra district, 12.1901, W. Forsyth (NSW); *Mt. Kosciusko, 7,000', 2.1890, W. Bäuerlen, n. 90 (MEL); Mt. Kosciusko, "above snowline", 1.1896, J. M.

Curran (NSW); *Mt. Kosciusko, 5,500' to summit, 1.1898, J. H. Maiden (NSW); Mt. Kosciusko, "Treeline to 7,000'", 1.1899, J. H. Maiden and W. Forsyth (NSW, BRI); Mt. Kosciusko, 1.1930, T. Harris (NSW).

Victoria: Mt. Hotham, C. Walter (MEL); Mt. Hotham, 1.1919, H. B. Williamson (NSW); Mt. Hotham, "summit", 1.1899, C. Walter (MEL); *Mt. Buller, 22.3.1853, F. Mueller (MEL); Victorian Alps, 1.1892, C.W. (BRI); Cobboras Mts., 6,000', F. Mueller (lecto-type, MEL); Mt. Wellington, 5,000', 11.1854, F. Mueller (MEL); Mt. Wellington, 12.1887, A. W. Howitt (MEL); Munyong Mts., 5,000'-6,000', 1.1855, F. Mueller (MEL).

Although the specimen selected as lectotype is undated, there seems no doubt that it is the one cited in the original description, with which it agrees in all particulars. Mueller's observation "often tinged with a purplish hue", is of no taxonomic significance



Text-figures 58-67. Fruit. $\times 17$ approx.

58, *B. aculeata*. 59, *B. marginata*. 60, *B. papillosa*. 61, *B. curvicarpa*. 62, *B. Muellerei*, inner surface of fruit. 63, *B. Muellerei*, outer surface of fruit. 64, *B. Muellerooides*, outer surface of fruit. 65, *B. Muellerooides*, inner surface of fruit. 66, *B. cardiocarpa*. 67, *B. nivalis*.

as this feature has been noted in the field on numerous occasions, and is displayed periodically by various different genera and families. It is probably correlated with deficiency of some particular mineral element in the soil. Examination of all fruiting capitula available has failed to confirm the dimorphism of the fruit recorded in the original description ("those of the disc very narrowly winged, those of the ray surrounded with a broad torn membrane"). It was found, however, that a large proportion of the disc fruit are undeveloped and never reach maturity. In this condition the wing is narrow and distorted by pressure from the earlier maturing fruit of the ray and outer disc florets, and it is probable that it is to these abortive fruit that Mueller's description of the disc fruit applies.

The only significant variation noted was in the case of the specimen from the Kiandra district. In this instance, although the fruit is typical in general appearance, the wing bears conspicuous and irregular flaps of tissue towards its inner margin. This feature was shown by nearly all the fruit present, but was not found on any other specimen.

B. nivalis is obviously closely related to *B. cardiocarpa*, the only distinguishing features as far as the fruit is concerned being the presence of short glandular hairs on the body, and a somewhat longer pappus. It is an exclusively alpine species of limited distribution, whereas *B. cardiocarpa* occurs at lower altitudes, mainly in swampy coastal areas.

Brachycome nivalis F. Muell., var. β *alpina* (F. Muell. ex Benth.) comb. nov.

(Text-fig. 57; Plate vi, map 21.)

Synonymy: *B. cardiocarpa* var. *alpina* F. Muell. ex Benth., Fl. Aust., iii (1866), 516. *B. Tadgellii* Tovey and Morris, Vict. Nat., xxxviii (1922), 135.

Lectotype: "In truly grassy places on the summit of Cobboras Mts.", 2.1854, F. Mueller (MEL).

Lectoparatypes: Two, l.c. (NSW).

Radical leaves broad linear to narrow spathulate, obtuse to subacute, entire or irregularly pinnatifid with linear obtuse to sub-acute lobes, 1.5–4.5 mm. long. Leaves on scapes linear, entire or with a few small lobes, up to 3 cm. long.

Range: Highlands of southern New South Wales and Victoria as far west as Mt. Baw-Baw.

Specimens examined:

New South Wales: Mt. Kosciusko, up to 5,500', 1.1898, J. H. Maiden (MEL); Kosciusko, "Treeline to 7,000", 1.1899, J. H. Maiden and W. Forsyth (BRI, NSW).

Victoria: Mt. Bogong, 12.1921, A. J. Tadgell (MEL); head of Bundarra R., near Mt. Jim, 5,900', Bogong High Plains, "among basalt rocks at the water's edge", 15.1.1946, J. H. Willis (MEL); Cobboras Mts., "turfy grassy places", 2.1852, F. Mueller (lectotype *B. nivalis* var. *alpina*, MEL; lectoparatypes, NSW); Mt. Hotham, 6,000', 12.1913, A. J. Tadgell (holotype and paratype *B. Tadgellii*, MEL); Mt. Hotham, 9.1921, *12.1921–1.1922, A. J. Tadgell (NSW, MEL); *North-east Mountains, 1895, C. Frost (MEL); Australian Alps, F. Mueller (MEL); *Munyang Mts., 1.1855, F. Mueller (MEL); Mt. Baw-Baw, 4-5,000', 12.1860–1.1861, F. Mueller (MEL).

Originally described as *B. cardiocarpa* var. *alpina*, this variety is now incorporated in *B. nivalis* without change of rank. This alteration is justified by the fact that the fruits are identical with those of *B. nivalis*, while they can readily be distinguished from those of *B. cardiocarpa* on the characters which separate these two species.

The syntype specimens of this variety bear entire leaves, but further collecting during recent years has produced others showing every gradation between plants in which an occasional leaf bears one or more lobes, to those in which the majority are pinnatifid. The varietal concept is accordingly extended to include these forms.

Examination of syntype specimens of *B. Tadgellii* shows that they are specimens of this variety bearing exclusively abortive fruit, thus confirming the opinion already held by Victorian botanists.

The fruits exhibit the same variation recorded for var. *nivalis* except in the case of the specimen collected by Mueller from the Australian Alps. Here the fruits, although nearly mature, do not show the characteristic broad wing, though in a few of them there is an indication of one distally.

Vegetative variation is sometimes considerable, but the general typical appearance of the plant as a whole is not altered. Specimens show every gradation between exclusively entire leaves, and those in which the majority are pinnatifid. Sometimes both extremes, with intermediates, are found in the same situation, which indicates that the variation is genetic rather than ecological or geographic.

5. Superspecies *DIVERSIFOLIA*.

30. *BRACHYCOME DIVERSIFOLIA* (Grah. in Hooker) Fisch. and Mey.

Ind. ii, Sem. Hort. Petrop. (1835), 31.

Erect or ascending perennials (?) up to 44 cm. high, branching from the base and above. Stems glandular and usually more or less conspicuously septate-hairy. Cauline leaves up to 9.5 cm. long, numerous, singly or doubly pinnatisect distally, narrow and entire proximally, with the base expanded but not sheathing. Ultimate segments linear to oblong, obtuse to acute, up to 1 cm. long, 3.5 mm. broad. Radical leaves, when present, similar to the cauline. *Peduncles* slender or robust, minutely glandular, leafy proximally. *Capitula* 1–25, up to 1.8 cm. diameter. *Involucral bracts* about 24, up to 9 mm. long, 3 mm. broad, linear-oblong to oblong, sub-acute to acute, the margins entire or microscopically serrulate. *Ray florets* up to 46, the rays 1.2 cm. long, 3 mm. broad, white. *Receptacle* 4 mm. broad, 3.5 mm. high, steeply conical, deeply pitted. Fruiting head hemispherical. *Fruit* up to 2–2.8 mm. long, 0.9 mm. broad, narrow-cuneate, quadrangular, light to very dark reddish-brown, rounded apically, laterally compressed, with two longitudinal folds on each side, and sometimes a few inconspicuous tubercles between them. Pappus bristles white, obliquely placed.

Key to the varieties.

1. Leaves cuneate in rough outline, singly pinnatisect var. *a diversifolia*
- 1.* Leaves doubly pinnatisect 2
2. Ultimate leaf segments thick, obtuse to oblong var. *β maritima*
- 2.* Ultimate leaf segments thin, linear to linear-oblong var. *γ dissecta*

Brachycome diversifolia (Grah. in Hooker) Fisch. and Mey., var. *a diversifolia*
comb. et stat. nov.

(Text-figs. 68, 77; Plate vi, map 22; viii, 2.)

Pyrethrum diversifolium Grah. in Hooker, Exot. Fl., ii (1823), 215.

Brachystephium leucanthemoides Less., Syn. Comp. (1832), 388.

Steiroglossa humilis DC., Prod. vi (1837), 38.

Brachycome diversifolia (Grah.) Fisch. and Mey., var. *humilis* Benth., F. Aust., iii (1866), 511.

Erect robust plants with up to five slightly branched or unbranched stems. Radical leaves few, usually absent. Cauline leaves numerous, with up to 11 oblong, sub-acute to acute segments. *Peduncles* usually robust. *Capitula* 1–6 up to 1.8 cm. diameter. *Ray florets* about 45.

Range: Highlands of New South Wales, south from Capertee, through Victoria to south-eastern South Australia.

Specimens examined:

New South Wales: Capertee, 1.1.1900, J. L. Boorman (NSW); *Piper's Flat, 12.1905, B. Wright (NSW); Sunny Corner, 11.1899, J. L. Boorman (NSW); Mt. Victoria, 1.1915, A. A. Hamilton (NSW); Blackheath, 4.1899, 1.1904, J. H. Maiden (NSW); Blackheath, 1.1903, A. A. Hamilton (NSW); Harefield, Groome (MEL); Jenolan Caves, 11.1899, W. F. Blakely (NSW, BRI); *Breadalbane, 9.1920, B. Harkins (NSW); Tumbarumba, 11.1900, W. Forsyth (NSW); Yarrangobilly Caves, 2.1897, E. Betche (NSW); Kiandra, 12.1901, W. Forsyth (NSW); Jindabyne, 1.1899, J. H. Maiden and W. Forsyth (NSW).

Victoria: Murray R., ? F. Mueller (MEL); Mt. Macedon, 4.1902, C. Walter (MEL); Braybrook, basaltic plains, 14.10.1897, W. R. Baker (MEL); Yarra R. (MEL); *Brighton, "on rocky sandy cliffs", 21.8.1853, S. G. Hannaford (NSW); *Sandringham, 10.1897, C. French Jnr., and C. Walters (MEL); *Dandenong Ranges, 19.12.1884, F. M. Reader (MEL); Skipton, W. J. Whan (MEL); *Ararat, C. Green (MEL); Grampians, 10.1904, Crowle (MEL); Grampians, 1869, Sullivan (MEL); *Dimboola, 25.9.1892, F. M. Reader (MEL); *Dimboola, 1.10.1942, W. Brand (NSW); Wimmera, Dallachy (MEL); Yarrambiak Crk., 13.11.1903, F. M. Reader (MEL); *Mouth of the Glenelg R., W. A. Hitt (MEL); *Victoria, F. Mueller (MEL).

Bass Strait: *Flinder's Island, 4.10.1847, Milligan, n. 1034 (MEL).

Tasmania: *Boat Hb., George's Bay, "sandy flat behind dunes", 10.11.1945, W. M. Curtis (HO); *N.E. Coast, "very scarce on sand", C. Stuart, n. 1032 (MEL); South Esk R., 12.1849, C. Stuart (MEL); South Esk R., 20.11.1849, C. Stuart, n. 152 (MEL); Remine, 12.1893 (NSW); Zeehan, 11.1891, L. Rodway (HO); Macquarie Harbour, 12.11.1842, Gunn, n. 694 (NSW); Tasmania, 10.1.1837, Gunn, n. 830 (NSW); *Tasmania, Archer (NSW); *Tasmania, C. Stuart (MEL).

South Australia: *Near Pt. Adelaide, 1850, Blandowsky (MEL); Forest Range, 14.10.1934, J. B. Cleland (JBC, JMB); Forrest Range, 18.11.1934, C. M. Eardley (AD); *Upper Sturt R., 21.10.1905, J. M. Black (JMB); Upper Holland's Creek, near Forrest range, "side of gully", 12.10.1946, J. B. Cleland (JBC); Belair, 2.1902, M. Koch (NSW); *between Belair and Blackwood, 'scrub, ligules white", 2.10.1909, J. M. Black (JMB); Brighton (BRI); Clarendon, 29.11.1881, R. Tate (AD); Mt. Compass, 12.10.1926, J. M. Black (JMB); Myponga, 15.11.1909, H. H. D. Griffith (JMB); Mt. Gambier, R. Tate (AD); *Mt. Gambier, Wehl (MEL).



Text-figures 68-70. Habit studies. $\times \frac{1}{3}$.

68, *B. diversifolia* var. *diversifolia*. 69, *B. diversifolia* var. *maritima*.
70, *B. diversifolia* var. *dissecta*.

Graham's syntype material of *Pyrethrum diversifolium* being at Kew, has not been examined by the author. There seems no doubt, however, that it is also syntype material for *Brachycome diversifolia*, Fischer and Meyer having redescribed the species from the original material. Lessing erected the monotypic genus *Brachystephium* for this species, listing *Brachycome diversifolia* as a synonym for the newly erected name *Brachystephium leucanthemoides*. Attempts to trace the specimens used by Lessing have been unsuccessful, but as his description applies satisfactorily, the synonymy of *Brachystephium leucanthemoides* and *Brachycome diversifolia* is accepted.

A lectotype of *Steiroglossa humilis* was selected from De Candolle's specimens at Geneva, a photograph, young fruits and florets of which were kindly sent for examination.

This specimen is accompanied by a label bearing the data: "Wet plains. Lachlan R., N. S. Wales, July 1817", in Cunningham's handwriting, which agrees with the locality data given in the original description. Bentham's description of *B. diversifolia* var. *humilis*, however, was based on duplicate specimens in the British Museum, so that it is from these that type selection for this variety should be made. Since it has not been possible to examine these particular specimens no lectotype has been designated for Bentham's variety.

Typical members of this variety are robust, relatively tall plants with large inflorescences and a conspicuous septate-hairy indumentum on the stems. These forms are apparently confined to the southern parts of the eastern States and Tasmania, for passing northward the plants become less robust, and the leaves and inflorescences smaller. It was on one of the latter forms that De Candolle based his description of *Steiroglossa humilis* ("Lachlan R., 7.1807, A. Cunningham"), and when Bentham later relegated it to a variety of *B. diversifolia* he gave the brief description "very small in all its parts, but not otherwise different, probably a starved state". The relatively small size shown by these specimens is probably to be correlated with some ecological factor, as a complete series is found between both extremes.

Although the lower cauline leaves are normally pinnatisect, it is not unusual to find a leaf in which a few of the segments are themselves irregularly toothed, or even pinnatisect. Leaves showing this condition are a very small minority of those present, and consequently have usually been overlooked. An interesting variation in habit is shown by some specimens from the Blue Mts. district (Mt. Victoria, 1.1915, A. Hamilton, Capertee, 1.1.1900, J. L. Boorman, and Blackheath, 4.1899, 1.1904, J. H. Maiden) in which 1-3 stems arise from the base and each of these branches dichotomously several times, the ultimate branches each terminating in an inflorescence. In the typical condition the original branches bear each a terminal inflorescence so that the number of inflorescences on a plant seldom exceeds four. The above-mentioned plants may be found to constitute a separate variety, as typical plants occur in the same locality, and this is not a character which is likely to be determined by ecological conditions.

A strong vegetative resemblance frequently exists between small plants of *B. diversifolia* and large plants of *B. goniocarpa*. This, together with the fact that the fruits of the two have much in common, indicates that the resemblance between them is based on close phylogenetic affinity. In both species the fruit is quadrangular and the conspicuous pappus obliquely placed; in *B. goniocarpa*, however, the pappus bristles are stellately arranged, while this is not usually so in *B. diversifolia*.

Brachycome diversifolia (Grah. in Hooker) Fisch. and Mey., var. β *maritima* Benth.,
Fl. Aust. iii (1866), 511.

(Text-fig. 69; Plate vi, map 22.)

Haptype: "Bass' Straits, R. Brown" (MEL ex BM).

An ascending much-branched plant up to 44 cm. high. Cauline leaves up to 8.3 cm. long, often doubly pinnatisect, the segments obtuse to sub-acute, obtusely to oblong, rather thick, up to 1 cm. long, 3.5 mm. broad. Radical leaves absent. *Capitula* up to 12, each about 1.5 cm. diameter. *Ray florets* up to 35.

Range: Islands of Bass Strait.

Specimens examined: Hogan Group, 28.11.1937, A. H. Mattingley (MEL); *Kent Group, 11.1890, Vic. Field Nat. Club (MEL); Deal Is., Kent Group, 1884, Dobson (MEL); Flinders Is., 4.10.1847, J. Milligan, n. 1034 (MEL); *Killcrankie Hill, Flinder's Is., "granite, 1,000'-1,200'", J. Milligan (MEL); Little Hummocky Is., 24.9.1884, J. Milligan, n. 610 (MEL); Goose Is., 25.1.1838, Gunn, n. 1145 (NSW); *Swan Is., 3.1888, Dobson (MEL); Bass Strait, 1802-5, R. Brown (haptype, MEL).

This variety was founded by Bentham on material collected by Robert Brown on the islands of Bass Strait; syntype material is at the British Museum. However, a specimen bearing the type caption was presented by that Institution to the National Herbarium, Melbourne, and has been nominated haptype.

The ascending habit of this variety is a unique character within this species, and a greater number of inflorescences is present than in var. *diversifolia*. The majority of

the leaves are doubly pinnatisect, but a few can usually be found on each plant which are singly pinnatisect.

All the specimens examined were well grown, which may explain the absence of radical leaves.

Brachycome diversifolia (Grah. in Hooker) Fisch. and Mey., var. γ *dissecta* var. nov.

(Text-fig. 70; Plate vi, map 22.)

Holotype: Darling Downs, Bybera, "sandy soil", 20.1.1936, C. T. White, n. 9703 (BRI).

Paratypes: Two, l.c. (NSW, MEL).

Herba erecta, a basi ramosa, ad 39 cm. alta. Folia radicalia et caulina, segmentis ultimis tenuibus linearibus-linearib-oblomis acuminatis ad 6 mm. longis, 1.7 mm. latis, bipinnatisecta. *Peduncululi* graciles. *Involucrici phylla* circiter 20, 6.5 mm. longa, 2 mm. lata, linearib-oblomis, sub-acuminata-acuminata. *Flores radii* circiter 20, ligulis 1 cm. longis, 1.5 mm. latis. *Receptaculum* 4 mm. latum, 3 mm. altum.

Erect plants branching from the base and above, up to 39 cm. high. Leaves radical and cauline, doubly pinnatisect, the ultimate segments thin, linear to linear-oblong, acute, up to 6 mm. long, 1.7 mm. broad. *Peduncles* slender. *Involucral bracts* about 20, 6.5 mm. long, 2 mm. broad, linear-oblong, sub-acute to acute. *Ray florets* about 20, the rays 1 cm. long, 1.5 mm. broad. *Receptacle* 4 mm. broad, 3 mm. high.

Range: Southern Queensland to Blue Mts. of New South Wales.

Specimens examined:

Queensland: Bybera, Darling Downs, "sandy soil, white flowers", 20.1.1936, C. T. White, n. 9703 (BRI, holotype; paratypes, MEL, NSW); Bybera, 3.9.1934, C. T. White (BRI).

New South Wales: Clarence R. (MEL); Glen Innes, 28.10.1886, E. Betche (NSW, MEL); Tingha, 6.1917, J. L. Boorman (NSW); Ebor Falls, 31.1.1941, Consett Davis (NSW); Nullo Park, Rylstone, 21.11.1938, A. S. North (NSW); Katoomba, 11.1932, W. F. Blakely (NSW).

This population is quite distinct from previously described varieties in the prolific branching, and greatly dissected leaves, a number of radical leaves being present in all specimens examined. Those from the type locality show a close vegetative similarity to specimens of *B. multifida* var. *dilatata* from the same district, but they can readily be distinguished vegetatively by the presence of radical leaves, and the expanded leaf bases.

31. BRACHYCOME SEGMENTOSA Moor. and F. Muell., Frag. Phytog. viii (1884), 144.

(Text-figs. 71, 78; Plate vi, map 22.)

Lectotype: "Lord Howe's Island. Summit of Mt. Gower, n. 89. Fullager and Lind." (MEL.)

Lectoparatypes: Five, l.c. (MEL).

Glabrous branching ascending (?) perennials up to 33.5 cm. high. Leaves cauline, pinnatisect, up to 4.3 cm. long, including the petiole. Lobes usually seven, cuneate, up to 1 cm. long, 5 mm. broad, acutely lobed or toothed distally. *Peduncles* terminal, with one or two linear bract-like leaves, otherwise naked. *Capitula* 3, 8 mm. diameter. *Involucral bracts* 5.5 mm. long, 2.2 mm. broad, about 14, obovate, glabrous, sub-acute, entire, marginally shortly ciliate. *Ray florets* about 30, up to 7 mm. long, 1.2 mm. broad, probably white. *Receptacle* 2 mm. broad, 1.5 mm. high, convex, deeply pitted. *Fruit* 2 mm. long, 1 mm. broad, cuneate, brown, flattened, with two longitudinal folds on each face which converge and unite distally. Pappus conspicuous, slightly excentric.

Range: *Recorded only from the type locality.

The small series of specimens available may be attributable not so much to the rarity of this species as to its isolated distribution in an area not greatly frequented.

This species shows definite affinities with *B. diversifolia*, but how this occurred is obscure, since geologists do not consider that Lord Howe Island was ever joined to the Australian mainland. Had this species occurred at sea level, its establishment could be more readily explained, but since it has been found only at an altitude of about 2,800 ft. it can only be suggested that fruit of *B. diversifolia* was carried there on the

* The following additional specimens of *B. segmentosa* have since been examined: *Summit of Mt. Gower, about 600 ft. below summit, 9.1908, C. Hedley and W. S. Dun (NSW); *Lord Howe Is., F. Mueller (NSW); *Lord Howe Is., 8.1911, W. W. Watts (NSW); Lord Howe Is., 12.1936, J. D. McComish (NSW).

feet of a bird. The possibility of this species having colonized the island first at sea-level and later migrated to the summit of Mt. Gower cannot be entirely overlooked. Had this occurred, however, it would be expected that plants would be found at other suitable localities. Further collecting may prove this to be the case. However the original colonization of Lord Howe Island took place, once the population became established the effects of isolation would, in time, lead to its diverging from the parent stock while still retaining certain similarities.

The main difference from *B. diversifolia* as far as the fruit is concerned is the somewhat smaller size and the fact that the pappus is not quite so asymmetrically placed. It is interesting to note the vegetative similarity between *B. segmentosa* and *B. diversifolia* var. *maritima*, both island populations. In both the leaves are doubly pinnatisect, but in the former species the segments are thin, while those of the latter are thick and almost leathery. This latter character, however, is one which might well be correlated with habitat, *B. diversifolia* var. *maritima* being found at sea-level, and *B. segmentosa* only at a high altitude.

32. BRACHYCOME GONIOCARPA Sond. and F. Muell., *Linnaea* xxv (1852), 475.

(Text-figs. 72, 79; Plate vi, map 23.)

Lectotype: Burra Mines, "near creeks and on the swampy meadows", 10.1852, F. Mueller (MEL).

A weakly erect to erect leafy (?) annual up to 22.5 cm. high, branching from the base, glandular and septate hairy. Leaves broadly sessile, pinnatipartite distally with 5-9 linear to broad-linear segments up to 4.3 mm. long, 1.7 mm. broad, obtuse to sub-acute, sometimes toothed. Cauline leaves few to many, sometimes crowded, up to 3 cm. long, often becoming entire distally. Radical leaves, when present, up to 4.3 cm. long. *Peduncles* more or less leafy. *Capitula* up to 100, 5-9 mm. diameter, in dwarf plants often exceeded by the upper leaves. *Involucral bracts* 10-25, 3-6 mm. long, 1-2 mm. broad, narrow obovate, sub-acute to acute with torn ciliate margins, sparsely glandular pubescent on the outer surface. *Ray florets* 13-22, the rays 4-8 mm. long, 1.2-2 mm. broad, apparently always white. *Receptacle* 1.5-2 mm. broad, 1.1-2 mm. high, hemispherical, moderately pitted. *Fruiting head* hemispherical. *Fruit* 1.2-2.4 mm. long, 0.5-2 mm. broad, black, cuneate, thick, quadrangular, with the lateral longitudinal folds broken up into tubercles; margins smooth, rounded distally or the dorsal one produced into a conspicuous crest. Pappus white, stellate and obliquely placed.

Habitat: Only three specimens are accompanied by ecological notes, two of them being from forest land with sandy soil.

Range: South-eastern Queensland through western districts of New South Wales and Victoria to southern parts of South Australia and Western Australia.

Specimens examined:

Queensland: Darling Downs, Bybera, "very common on forest land, rather sandy soil", 20.9.1944, C. T. White, n. 12619 (BRI).

New South Wales: Paroo River, 9.1900, E. Betche (NSW); Paroo R., Spring, 1941, N. C. W. Beadle (NSW, BRI); Narrabri, 11.1899, J. H. Maiden (NSW); Narrabri, 25.11.1916, J. B. Cleland (JBC); Pilliga, "covering iron bark and pine lands. Sandy Creek bed", 9.1913, E. H. F. Swain (NSW); Pilliga, 8.1921, C. Beckhaus (NSW, BRI); Moonbi, 10.1886, E. Betche (NSW); Bowan Park, near Cudal, 10.1906, W. F. Blakely (NSW); *Cowra, 9.1915, J. Beattie (NSW); Condobolin, J. H. Maiden (NSW); Wyalong, 10.1903, 22.9.1906, J. L. Boorman (NSW); *Wyalong, 3.9.1915, J. W. Dwyer (NSW); Barmedman, 10.1916, J. W. Dwyer (NSW); Yanco, 5.10.1912, J. B. Cleland (JBC); Hay, 22.9.1889, J. J. Fletcher (NSW); Wagga, 10.1896, J. H. Maiden (NSW); Wagga, J. J. Fletcher (NSW); Gilmore, near Tumut, 10.1916, J. L. Boorman (NSW).

Victoria: *Murray River, near Albury, 1890, J. Wilson (MEL); *Barnawartha, W. G. Fuller (MEL); Murray River, mallee scrub (MEL); Lake Albacutza, mallee, 10.1899, C. Walter (NSW); Dimboola, 30.8.1891, F. M. Reader (MEL).

South Australia: Fowler's Bay (JMB); Yalata, Fowler's Bay, R. Tate (AD); Davenport Creek, E.P., 20.8.1923, J. B. Cleland (JBC); Burra Mines, "near creeks and on sandy meadows", 10.1852, F. Mueller (lectotype, MEL); Mt. Lofty Ranges, F. Mueller (MEL); Enfield, 10.1850, F. Mueller (MEL); near Monarto South, 7.10.1926, J. B. Cleland (JMB); Kinchina, 8.11.1924, 10.1926, 9.1927, J. B. Cleland (JMB, JBC); Murray Plain, 8.1881, R. Tate (AD); ? south east (JMB); *Bordertown, 14.9.1908 (JMB), Bordertown, 9.10.1911, Turner (JMB); Edward's River, 10.1875, F. Mueller (MEL, NSW).

Western Australia: Flat Rock, Salt River, 10.1903, C. Andrews (PERTH).

Only one specimen from the type locality pre-dating the original description having been traced, this was nominated lectotype. The observation in the original description "fruit often blackish" is explained by the fact that a large number of those present are immature and consequently have not yet attained the characteristic black colour. An accurate description of the disc fruit is given in the original description, but that of the ray fruit is based on immature ones, "Ray fruit more slender, ciliolate at margins". It has been found that although dimorphism, in the strict sense, does not exist, the shape of the fruit can be correlated with their position on the receptacle. Not only does their curved nature become more exaggerated towards the periphery, but the dorsal margin, which typically is rounded towards the apex, tends to become acute and sometimes rises in a peak.

The fruits of the lectotype bear on each side two conspicuous longitudinal rows of tubercles united distally by a curved fold. Both outer and inner margins are smooth, the former curving inwards to the obliquely placed pappus. There is no conspicuous distinction between fruit occupying the periphery of the receptacle and the inner ones, though the former may be slightly broader. The specimens from Queensland and northern New South Wales, however, show an interesting variation in that the peripheral fruit have the dorsal margin almost horned distally, becoming acute, and finally rounded in the fruit passing towards the centre of the capitulum.

Vegetative variation is limited to the size of the plant, the smallest flowering specimen seen being 1.2 cm. high, with leaves correspondingly reduced in size. A number of these dwarf plants have been examined (Dimboola, Yalata, Davenport Creek, Kinchina and Bordertown), and in the absence of collector's notes it is assumed that their size has an ecological basis.

In the thick fruit with an asymmetrical pappus a close affinity is seen with *B. diversifolia*, both species belonging to the same line of descent. In the latter, the longitudinal folds are continuous and not very conspicuous, but in *B. goniocarpa* a strong tendency is apparent leading to the breaking up of these folds into large tuberculate structures. It is probable that *B. goniocarpa* originated directly from *B. diversifolia* on the mainland of Australia (possibly Victoria) and for that reason has been prevented from reaching Tasmania.

33. BRACHYCOME READERI SP. NOV.

(Text-figs. 73, 80; Plate vi, map 24.)

Holotype: Wannon Valley, 10.11.1902, H. B. Williamson (MEL).

Paratypes: Four, l.c. (MEL).

Herba annua, glabra, infirme erecta, nullo principe caule ad 13 cm. alto. Folia radicalia ad 7.5 cm. longa, 1.6 cm. lata, linearis, acuminata, integra aut 1.2 dentata plerumque adsunt. Folia caulina ad 6.2 cm. longa, lobis 3-5 in apice linearibus, acuminatis ad 8 mm. longis 1.1 mm. latis plerumque pinnatisecta. *Pedunculi* basi foliosi. *Capitula* 1-6 transverse lata 7 mm. *Involucri phylla* circiter 14, 3-5 mm. longa, 1-1.5 mm. lata, oblanceolata, obtusa-subacuminata, nunc integra nunc dentibus minimis. *Flores radii* 10-16, ligulis circiter 6 mm. longis, 2.5-2.8 mm. latis, verisimiliter albis. *Receptaculum* 2 mm. latum, 1.5 mm. altum, conicum, paulum punctum. *Capitulum fructuosum* hemisphaericum. *Achaenia* 1.5 mm. longa, 1 mm. lata, fusca, late cuneata, crassa; superficiebus lateralibus sinus 2 conspicui longi tuberculatusculi in apice iuncti margines ventrales dorsualesque in apice acuminati. Pappus clarus, stellatus in medio positus.

Glabrous, weakly erect annuals (?) up to 13 cm. high with no main stem. Radical leaves usually present, up to 7.5 cm. long, 1.6 mm. broad, linear, acute, entire or with 1-2 teeth. Cauline leaves up to 6.2 cm. long, usually pinnatisect, with 3-5 distal linear acute segments up to 8 mm. long, 1.1 mm. broad. *Peduncles* leafy proximally. *Capitula* 1-6, about 7 mm. in diameter. *Involucral bracts* about 14, 3-5 mm. long, 1-1.5 mm. broad, oblanceolate, obtuse to sub-acute, the margins entire or minutely serrulate. *Ray florets* 10-16, the rays about 6 mm. long, 2.5-2.8 mm. broad, apparently white. *Receptacle* 2 mm. broad, 1.5 mm. high, conical, slightly pitted. *Fruiting capitulum* hemispherical. *Fruit* 1.5 mm. long, 1 mm. broad, brown, broadly cuneate, thick; lateral surfaces bearing

two conspicuous more or less tuberculate longitudinal folds united distally; dorsal and ventral margins acute apically. Pappus conspicuous, stellate, centrally placed.

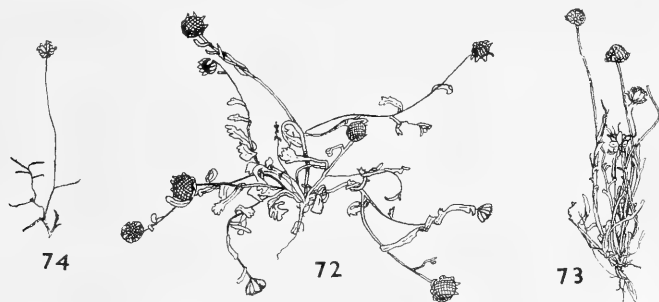
Range: Victoria, mainly western districts.

Specimens examined: Nathalia, 10.1930, J. H. Willis (MEL); Wannon River, 10.1903, H. B. Williamson (MEL, BRI); Wannon Valley, 10.11.1902, H. B. Williamson (MEL, holotype, paratypes); Peshurst, 11.1907, H. B. Williamson (MEL); south-west Victoria, 3.1901, H. B. Williamson (NSW).

The sheet bearing the type series is labelled by F. M. Reader as a new variety of *B. goniocarpa*, but publication of the name was not effected. As the manuscript name is already occupied by a New Zealand species, it is named after the collector.

All specimens examined were strikingly similar in every way, the only variation noted occurring in the specimens from S.W. Victoria, in which the margins of the ray and outer disc fruit are horned apically, a condition observed in certain specimens of *B. goniocarpa*.

This species is most closely allied to *B. goniocarpa* both in general mode of growth and fruit structure. It can, however, be readily distinguished in the vegetative stage by its relatively long leaves with linear segments, and its glabrous nature. The longitudinal folds present on the fruit are not broken up into tubercles as in *B. goniocarpa* and the pappus is centrally placed instead of being oblique. In both species the fruiting capitulum is hemispherical.



Text-figures 72-74. Habit studies. $\times \frac{1}{2}$.

72, *B. goniocarpa* (Lectotype). 73, *B. Readeri* (Holotype). 74, *B. eriogona* (Paratype).

34. BRACHYCOME ERIOGONA (J. M. Black) comb. nov.

(Text-figs. 74, 81; Plate vi, map 24.)

Synonymy: *B. goniocarpa* var. *eriogona* J. M. Black, *Proc. Roy. Soc. S.A.*, li (1928), 228.

Holotype: Near Lake Frome, 12.1920, S. A. White (JMB).

Paratype: l.c. (JMB).

Erect branching glabrous (?) annuals, 5.4-8.5 cm. high. Leaves cauline, pinnatisect, up to 1.5 cm. long, the segments narrow-linear, acute, up to 3.5 mm. long, 0.2-0.5 mm. broad. *Peduncles* leafy proximally. *Capitula* up to 10, 4-4.5 mm. diameter. *Involucral bracts* 2-2.5 mm. long, 0.6-1.5 mm. broad, oblanceolate, obtuse to sub-acute, entire, glabrous. *Ray florets* apparently about 18. *Receptacle*: apparently hemispherical. *Fruit* light brown, 1.5-2 mm. long, 0.5-1 mm. broad, roughly cuneate in outline, curved, with a broad fold running down each side bearing a longitudinal band of glandular hairs. Pappus conspicuous and stellate.

Range: Lake Frome region, represented by only the syntype specimens.

Originally described by Black as a variety of *B. goniocarpa*, the characters shown by the only two specimens known are such as to warrant specific status. Unfortunately these specimens are in a bad state of preservation, and as certain details such as the size of the rays and the receptacle could not be obtained without inflicting further damage, it was decided to await the collecting of further material before recording these.

This species is most closely allied to *B. goniocarpa*, of which it may prove to be a geographic subspecies. Both species have the same mode of growth and type of fruit,

but *B. eriogona* can be immediately distinguished by its glabrous nature, the narrow-linear acute leaf segments, and the entire involucrel bracts. The fruits, unfortunately, are not fully mature, but resemble those of *B. goniocarpa* at a similar stage of development. They are, however, distinct in their rather woolly appearance, due to the presence of long glandular hairs, in their curved, instead of cuneate, outline, and in the fact that the pappus bristles, though the same length as those of *B. goniocarpa*, are not stellately arranged.

6. Superspecies TESQUORUM.

35. BRACHYCOME TESQUORUM J. M. Black, *Proc. Roy. Soc. S.A.*, XI (1916), 75.

(Text-figs. 75, 82; Plate vi, map 24.)

Lectotype: Oodnadatta, 1.1913, Miss Staer (JMB).

Erect glandular-pubescent perennials up to 16.5 cm. high, branching from the base. Leaves cauline, oblanceolate, sessile, up to 2.5 cm. long, 4 mm. broad, entire or bearing lateral narrow-linear to filiform teeth. *Peduncles* robust, naked. *Capitula* up to 6–8 mm. diameter, 14 present on lectotype. *Involucrel bracts* 16–18, 3–5 mm. long, 1.2 mm. broad, oblong, acute, with torn-ciliate margins. *Ray florets* about 25, the rays 5 mm. long, 1 mm. broad. *Receptacle* slightly convex, 1 mm. broad, 0.5 mm. high, moderately pitted. *Fruit* 1.7–2 mm. long, 0.6 mm. broad, narrow-obovate, brown, flattened, with two longitudinal



Text-figures 71, 75, 76. Habit studies. $\times \frac{1}{3}$.

71, *B. segmentosa* (Lectotype). 75, *B. tesquorum* (Lectotype). 76, *B. Blackii* (Holotype).

folds on each face, and with numerous curled glandular hairs which are very short distally. Pappus absent.

Range: Confined to Central Australia.

Specimens examined: Glen Ferdinand, Musgrave Ranges, 18.7.1914, S. A. White (JMB); Oodnadatta, 1.13, — Staer (lectotype JMB).

This species is known only from the syntype series, no further specimens having been collected since the original description. It is recorded only from Central Australia, and it would appear to be rare. In such a short series no comments can be made on intra-specific variation, and its affinities are obscure.

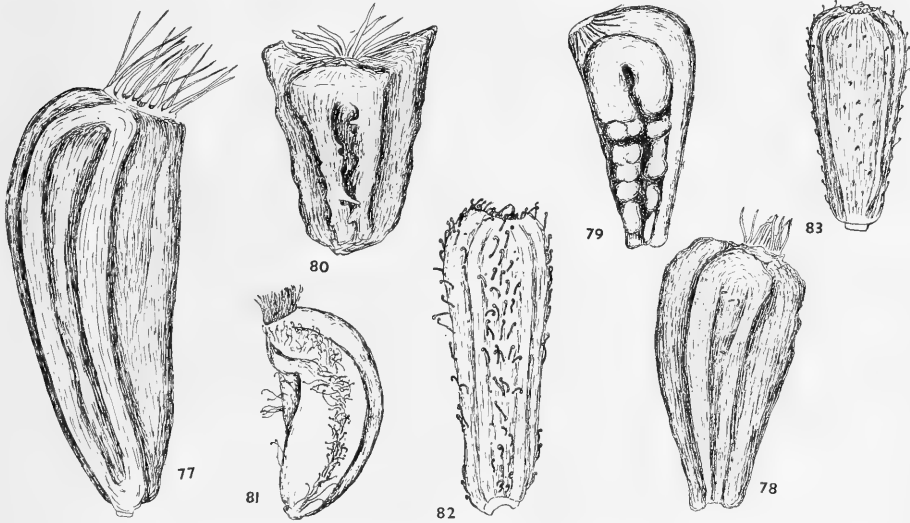
36. BRACHYCOME BLACKII SP. NOV.

(Text-figs. 76, 83; Plate vi, map 24.)

Holotype: Reedy Creek, Central Australia, "Lax, spreading 2-3 ft.". 1894, R. Tate, Horn Expedition (AD).

Paratypes: Two, Palm Creek, rocks, R. Tate. Horn Expedition (AD, NSW).

Herba perennis, ramosissima, ad 37 cm. alta, omnino breve glanduloso pilosa. Folia caulina, sessilia, inferiora ad 1.8 cm. longa, bipinnatifida, lobis primis 2-4 mm. longis, 1 mm. latis, acuminatis, in apice integris, inaequaliter dentalis aut lobatis, in basi filiformibus et integris. *Peduncululi* ad 7 cm. longi, vel nudi vel 1-4 parvis foliis pinnatifidis.



Text-figures 77-83. Fruit. $\times 17$ approx.

77, *B. diversifolia*. 78, *B. segmentosa*. 79, *B. goniocarpa*. 80, *B. Readeri*.
81, *B. eriogona*. 82, *B. tesquorum*. 83, *B. Blackii*.

Capitula circiter ad 50 transverse lata 6 mm. *Involucri phylla* 10-14, subacuminata-acuminata, fimbriato-ciliatis marginibus, dense glanduloso-pilosa, 4-5.1 mm. longa, 1.2-2 mm. lata, obovata-oblancoolata. *Flores radii* 40-58, ligulis 6 mm. longis, 0.8 mm. latis, caeruleis etiam albis. *Receptaculum* transverse latum 0.9-1.3 mm., 0.9-1.3 mm. altum, convexum, vix punctum. *Achaenia* 1.6 mm. longa, 0.8 mm. lata, anguste-cuneata, compressa, levia, paucis pilis volutis, fulva. Pappus mic.

Freely branching perennials (?) up to 37 cm. high, shortly glandular-hairy all over. Leaves cauline, sessile, the lower up to 1.8 cm. long, bipinnatifid; primary lobes 2-4 mm. long, 1 mm. broad, acute, entire or irregularly toothed or lobed, the proximal lobes filiform and entire. Upper leaves 4-6 mm. long, pinnatifid with linear lobes. *Peduncles* up to 7 cm. long, naked or bearing 1-4 small pinnatifid leaves. *Capitula* up to about 50, 6 mm. diameter. *Involucral bracts* 10-14, sub-acute to acute, with torn-ciliate margins, densely glandular-pubescent, outer ones 4-5.1 mm. long, 1.2-2 mm. broad, obovate to oblanceolate. *Ray florets* 40-58, the rays 6 mm. long, 0.8 mm. broad, "blue, also white". *Receptacle* 0.9-1.3 mm. diameter, 0.9-1.3 mm. high, convex, scarcely pitted. *Fruit*

1.6 mm. long, 0.8 mm. broad, narrow-cuneate, flattened, smooth with a few scattered apically rolled hairs, golden brown. Pappus microscopic.

Range: Central Australia.

Specimens examined:

Central Australia: Glen Helen Gorge, 1894, R. Tate, Horn Expedition (AD); Palm Creek Rocks, 1894. R. Tate, Horn Expedition (paratypes, AD, NSW); Reedy Creek, 1894, R. Tate, Horn Expedition (holotype, AD); Tempe Downs, 1894, R. Tate, Horn Expedition (AD); Govern, N.W. Exped., 1903, H. Basedow (NSW).

The majority of the specimens examined bore flowers or empty receptacles, but prolonged search revealed a few fruits which, if not fully mature, are at least nearly so.

This species is apparently widespread in Central Australia, and characters of the fruit show a close affinity with *B. tesquorum*, which is also confined to Central Australia. The fruits of both species are narrow-cuneate, thick and flattened, with indications of two longitudinal folds on each face. In both, scattered curled glandular hairs are present which, in other species, is usually an indication of immaturity. No pappus could be found in *B. tesquorum*, though it may have been obscured by the glandular hairs in this region, while in *B. Blackii* a definite though microscopic pappus is present. Vegetatively there is no similarity between the two species, *B. Blackii* showing a strong superficial similarity to certain specimens of *B. ciliaris*.

This species is named after Mr. J. M. Black, who has made outstanding contributions towards our knowledge of the Australian flora.

Subgenus METABRACHYCOME.

7. Superspecies IBERIDIFOLIA.

37. BRACHYCOME IBERIDIFOLIA Benth., Enum. Pl. Hueg., 59, No. 58 (1837).

(Text-figs. 84, 97; Plate vi, map 25.)

Synonymy: *B. iberidifolia*.

Var. *Huegeliana* Steetz in Lehmann, Pl. Preiss (1845), 425.

Var. *major* Steetz in Lehmann. Ibid.

Var. *alba* Steetz in Lehmann. Ibid.

Var. *divergens* Steetz in Lehmann. Ibid., 426.

Var. *diffusa* Benth., Fl. Aust., iii (1866), 513.

Var. *glandulifera* J. M. Black, Proc. Roy. Soc. S.A., lii (1928), 228.

Type: Swan River, Huegel (KEW ex herb. Vindl.).

Erect branching plants up to 41.5 cm. high, more or less glandular pubescent, occasionally glabrous. Leaves cauline, pinnatisect or rarely entire, up to 8 cm. long; segments up to 1.3 cm. long, 0.8 cm. broad, narrow- to broad-linear, obtuse to sub-acute, rarely with a short lateral lobe. *Peduncles* up to 8.5 cm. long, naked distally. *Capitula* 1-55, 5-7 mm. diameter. *Involucral bracts* 12-30, 1.7-4.4 mm. long, 0.7-1.8 mm. broad, oblong, sub-acute to acute, glabrous or sparsely glandular, the margins entire or minutely serrulate. *Ray florets* 8-22, the rays 6-16 mm. long, 1.5-4 mm. broad, white or violet. *Receptacle* 0.5-2 mm. broad, 0.7-1.5 mm. high, broadly convex to steeply conical, hardly pitted. *Fruit* 1.1-1.7 mm. long, 0.4-0.8 mm. broad, dark brown with minute tessellations at maturity, giving it a greyish appearance, narrow clavate, slightly flattened; central area sometimes slightly depressed between two conspicuous longitudinal ridges; curled hairs present distally. Pappus microscopic to minute, coroniform.

Range: Northern portions of South Australia and Bunda Cliffs to Western Australia.

Specimens examined:

South Australia: *Musgrave Ranges, 7.1926, H. Basedow (lectotype and lectoparatypes of *B. iberidifolia* var. *glandulifera*, JMB); *east of Everard Ranges, 17.8.1914, S. A. White (JMB); *Wynbring, 5.9.1920, E. H. Ising (JMB); *Bitter Well, Coondambo, 29.10.1929, J. B. Cleland (JMB); 25 miles N. of Pt. Augusta, 28.10.1929, J. B. Cleland (JBC); *Bunda Cliffs, "sandy soil", 1879, R. Tate (MEL).

Western Australia: Between Gascoyne and Forescue R., 1885, H. S. King (MEL); Wandagee, Minilya R., "rays white", 8.10.1914, C. A. Gardner, n. 6187 (PERTH); Gascoyne R., 1882, Pollack (MEL); Gascoyne R., 1882, J. Forrest (MEL); 60 miles E. of Carnarvon, 19.9.1941, C. A. Gardner, n. 6039 (PERTH); Carnarvon, 1893 (NSW); between Victoria Springs and Waring, 9.10.1875, Young (MEL); Lakeside, 8.1898, W. V. Fitzgerald (NSW); Merredin, 9.10.1923, M. Koch (MEL, NSW); *Tammin, "dwarf plant, flowers white, yellow sand on heath", C. A. Gardner, n. 6453 (PERTH); Moora, 10.1908, J. B.

Cleland (NSW); Gingin, "ray florets blue", 1.10.1933, W. E. Blackall (PERTH); Kelmescott, 6.11.1898, R. Helms (NSW); Guildford, "swampy ground", 23.11.1901, C. Andrews (PERTH); Midland Junction, 1902, A. G. Hamilton (NSW); Swan district, "On chalky hills near the sea", 11.1900 (NSW, AD); Swan R., near Point Walter, "in clayey, rather humid shady places among high grass on the bank of the river", 18.7.1839, L. Preiss, n. 97 (lectotype and lectoparatypes of *B. iberidifolia* var. *alba*, MEL); Perth, "in calcareous soil near Limekilns", L. Preiss, n. 95 (lectotype and lectoparatype of *B. iberidifolia* var. *major*, MEL); North Beach (NSW); Cottesloe Beach, 1902, A. G. Hamilton (NSW); near Fremantle "in turf spots near the Swan River", L. Preiss, n. 94 (lectotype and three lectoparatypes of *B. iberidifolia* var. *Huegeliana*, MEL); Fremantle, "sand", Oldfield (MEL); Serpentine, 1902, A. G. Hamilton (NSW); Murray R., Oldfield (MEL); Pinjarra, Murray R., 23.9.97, R. Helms (PERTH); Geographe Bay, Oldfield (MEL); Busselton, 1916, F. Stoward (PERTH); Vasse R., Oldfield (MEL); Vasse R., Preiss (MEL); Vasse district, L. Preiss, n. 96 (lectotype of *B. iberidifolia* var. *divergens*, MEL); Blackwood R., 1886, Hard (MEL); Blackwood R., "Flowers white to deep blue", Oldfield (MEL); Gooseberry Hill, Darling Range, 21.10.97, R. Helms (NSW); Manjimup, 11.20, M. Koch (MEL); Wooroloo, "white", 9.07, M. Koch (NSW); *Wooroloo, "rays conspicuous, bluish", 8.07 (NSW, MEL); Tone R., 20.12.59 (MEL); Salt R. (MEL); Oldfield R., "flats" (MEL); S.W. Aust., Maxwell (MEL); W.A., 1902, A. G. Hamilton (NSW); W.A., "ray almost black", J. Drummond (MEL); W.A., J. Drummond, n. 371 (MEL); W.A., L. Preiss, n. 94 (MEL).

The type of this species is at Kew and consequently not available for examination. In the Perth Herbarium there is a specimen from Pinjarra, Murray R., which bears the caption "matched Type: Swan River, Huegel, Hb. Kew, ex herb. Vindl, 1837, C. A. Gardner". This specimen has mostly entire, linear leaves, only occasional ones bearing one or two lobes. In view of Bentham's statement in his original description, "leaves pinnatisect", this specimen has not been used as a basis of comparison for all specimens as would otherwise have been done.

The varieties described by Steetz (Pl. Preiss, 425-6, 1845) were rejected by Bentham (1866) and examination of syntype material confirms this action. Unfortunately syntype material of var. *diffusa* Benth. has not been available for examination, but Bentham's description indicates that it, too, was based on unreliable criteria: "More branching from the base, achenes apparently flatter, but not seen ripe", and consequently is not confirmed in varietal status.

An examination of syntype material of var. *glandulifera* J. M. Black revealed the fact that the fruiting specimens are, in effect, *B. exilis* Sond. There are, however, flowering specimens of this series from Musgrave Ranges, Coondambo, Wynbring, and Everard Ranges which are apparently *B. iberidifolia*. The specimen from the former locality was accordingly selected as lectotype of Black's variety, but the variety itself was abandoned since it was discovered that the glabrous nature of the species was more apparent than real, and few specimens can be found to which the term "glabrous" can be strictly applied. In Steetz's description of var. *Huegeliana*, he quotes only one specimen: "on turf spots near the Swan River, not far from the town of Fremantle, 16.12.1838, Herb. Preiss, No. 94", and adds the comment, "This absolutely the Huegelian plant which I saw in the Herbarium at Vienna". This remark is taken to imply that Steetz considered this specimen identical with that collected from the Swan River by Huegel, which is the type specimen of the species, so that "var. *Huegeliana*" should really read "var. *typica*". In his original description Bentham states that the specimen is "quite glabrous", and subsequently confirms this observation in *Flora Australiensis* (iii, 512), yet examination of the specimen selected as lectotype of var. *Huegeliana* shows that the upper portions of the specimen are glandular pubescent. This specimen was examined by Bentham prior to the publication of *Flora Australiensis*, and it can only be assumed that its glandular nature was overlooked by him.

The author is indebted to Mr. J. S. L. Gilmour of Kew for the following information: "The type specimens (there are three on the sheet) of *B. iberidifolia* Benth. all possess glandular pubescence, although this is rather irregularly distributed and quite absent from some parts. All the leaves are pinnatisect, usually very obviously so, but in some of the lowest leaves the segments are restricted to the apical portion and comparatively short". In view of the above details of the indumentum present on the syntype specimens, Black's variety is rejected, based as it is on a character normally present though

originally unrecorded. All degrees of glandular pubescence have been noted, from specimens in which it is apparent only on young leaves and buds, to those in which the glandular nature can be detected macroscopically, and so far all attempts to correlate the variation of this character with environmental factors have failed.

Since syntype material has not been examined by the author, a lectotype has not been selected.

Variation is mainly confined to the size of the leaf segments and inflorescences, but specimens from three localities (Bunda Cliffs, Lakeside, Guildford) have been noted in which the leaves are all entire, and in two instances (Pinjarra, Merredin) both types of leaves are present.

Two folders of specimens were examined from Sharks Bay (10.1877, F. Mueller MEL) and one from "between Murchison River and Sharks Bay", which vegetatively are identical with *B. iberidifolia*. The fruits, however, are somewhat flattened, and on each face are two longitudinal ridges united distally by an expanded area. Between the ridges are a few small tubercles, and short curled hairs occur at the margins of the fruit. On the specimens in two of the folders a distinct, though short, stellate pappus is seen, but in the second folder from Sharks Bay there is no trace of a pappus, though the fruits are identical in other respects. Further specimens, from Ashburton and Cane Rivers (1878, A. Forrest MEL) bear fruits of a similar shape but tubercles are not present, the pappus is much larger, white and not stellate, and relatively long straight hairs occur between the longitudinal folds and at the margins of the fruit. *B. iberidifolia* has never been recorded from Queensland, but a specimen has been seen from Mulligan River, W.Q. (2.04, H. Clarke NSW), which is vegetatively identical. Unfortunately the fruits are not fully mature, but they show some distinct differences from the typical form in that the fruits bear numerous small straight hairs, and a microscopically minute pappus.

Characters of the fruit of the above specimens are beyond the normal limits of variation in *B. iberidifolia*, and as such are not included in the list of specimens examined. It may well be that they represent one or more new species, but until further specimens come to hand their variation from the typical condition is merely recorded.

38. BRACHYCOME BILLARDIERI Benth., Fl. Aust., iii (1866), 518.

(Text-fig. 85.)

Lectotype: Western Australia, J. Drummond, No. 374 (MEL).

An erect branching glabrous (?) perennial, 16 cm. high. Leaves cauline, sessile, cuneate in gross outline, pinnatisect and crowded. Lower leaves up to 1.5 cm. long, the lobes 2-2.5 mm. long, 1-1.5 mm. broad, shortly mucronate. *Peduncles* mainly terminal, sparsely glandular hairy, leafy proximally. *Capitula* about 12, 7 mm. diameter. *Involucral bracts* about 17, narrow oblong, bluntly acute, with entire, shortly ciliolate margins, 3 mm. long, 0.9 mm. broad minutely glandular. *Receptacle* conical, 1 mm. across the base, 0.7 mm. high. *Fruit* absent from the specimen.

This specimen is the only one in any Australian herbarium, and is consequently selected as lectotype, as it is apparently one of the specimens on which Bentham based his description from which the following remarks are quoted: "Achenes very flat, oblong, those of the ray apparently with thickened obtuse margins, those of the disk with the margins more acute and slightly ciliate or denticulate, but not seen perfect. Pappus minute or almost none."

As this particular specimen bears several empty receptacles, it is probable that Bentham removed what fruits there were for examination and that they were subsequently lost. Whether this is actually a valid species or not remains to be determined when further and more complete specimens are collected.

A further syntype specimen is reported to be at Kew, but as this has not been examined by the author specific type designation cannot be applied to it. No exact locality data accompany the lectotype, but it was probably collected in the vicinity of Perth.

39. BRACHYCOME TATEI J. M. Black. *Proc. Roy. Soc. S.A.*, lii (1928), 227.

(Text-figs. 86, 98; Plate vi, map 26.)

Lectotype: *Eucla, Batt. (AD).*Homoetype*: l.c. (MEL).

Branching and straggling plants with a minutely glandular pilose indumentum. Largest specimen examined 7.5 cm. high, but not complete. Leaves cauline, crowded, spatulate, rather thick and apparently fleshy, 0.8–2 cm. long, 4–8 mm. broad distally,

Text-figures 84-88. Habit studies. $\times \frac{1}{3}$.

84, *B. iberidifolia*. 85, *B. Billardieri*. 86, *B. Tatei*. 87, *B. parvula* var. *parvula* (Haptotype of var. Hook. f.). 88, *B. parvula* var. *lissocarpa* (Lectotype).

entire, crenate or obtusely pinnatifid, the midrib not apparent; leaf-blade tapering into the broad, slightly stem-clasping base. Lower stem woody, and bearing persistent bases of leaves. *Peduncles* axillary up to 1.5 cm. long, naked, slightly exceeding the leaves. *Capitula* up to 11, 6–7 mm. diameter. *Involucral bracts* about 14, linear-obovate to obovate, obtuse, 3.4 mm. long, 1.3–1.6 mm. broad, entire, marginally shortly ciliolate, glandular pilose on the outer face. *Ray florets* about 25, the rays 4 mm. long, 1.2 mm. broad. *Fruit* flat, 1.4 mm. long, 1 mm. broad, broadly obovate; central body greenish-black, the margins greenish-yellow, irregularly and shortly lobed or almost entire. *Pappus* a ring of microscopic teeth.

Range: Shores of Great Australian Bight from Fowler's Bay to Eucla.

Specimens examined:

South Australia: *Bunda Cliffs, R. Tate (AD); "Stony places, top of Bunda Cliffs", 12.2.79, R. Tate (MEL).

Western Australia: *Eucla, Batt. (lectotype, AD); Eucla, Batt. (homoeotype, MEL).

Since the syntype series is limited to a fragment from Eucla, and a larger specimen from Bunda Cliffs, neither of which bears mature fruit, it was decided to select the former specimen as lectotype and nominate a tototypical homoeotype bearing mature fruit. Such a specimen was found in the National Herbarium, Melbourne, and is very probably the original specimen from which Mueller removed the fragment now in the Tate Herbarium, Adelaide University. Evidence in support of this is that the specimen at Adelaide is accompanied by a locality label bearing Mueller's writing. As Black did not know of the existence of this second Eucla specimen, and consequently did not examine it, it does not form part of the syntype series. His description of the fruits is consequently inaccurate, as the only specimens known to him bear very immature fruit.

Owing to the paucity of specimens, no comment can be made on variation in this species, and its affinities can only be surmised. It is possible that collecting along the coast between Spencer's Gulf and Bunda Cliffs may lead to the discovery of forms intermediate between *B. Tatei* and *B. parvula*, with which species *B. Tatei* seems most closely allied.

40. BRACHYCOME PARVULA Hook. f., Fl. Tas. i (1860), 185.

Weakly erect branching plants, annual or perennial, up to 39 cm. high, glabrous or glandular hairy distally. Leaves radical and cauline, only the latter present in larger specimens. Radical leaves up to 7 cm. long, oblanceolate, obtuse and entire, or with 3-5 distal, irregularly arranged, linear, acute lobes up to 1.1 cm. long, 1.2 mm. broad, the terminal lobe slightly exceeding the lateral ones; proximal lobes sometimes reduced to filiform teeth. Cauline leaves few or numerous, entire or rarely bearing a few short teeth, up to 3.2 cm. long, 2.5 mm. broad, sessile, oblanceolate, linear or pinnatisect; when pinnatisect, leaves up to 10 cm. long with 3-5 linear, acute to sub-acute segments, up to 1.1 cm. long, 1.2 mm. broad. *Peduncles* naked or leafy proximally, glabrous or shortly glandular pubescent. *Capitula* up to 40, 7-9 mm. diameter. *Involucral bracts* about 20, 2-3.5 mm. long, 1-1.5 mm. broad, narrow-oblong, glabrous or minutely pubescent, obtuse, more or less torn-ciliate apically. *Receptacle* hemispherical, 2.6-3 mm. broad, 1.5-2.5 mm. high, moderately pitted. *Ray florets* 40-80, the rays 3-5 mm. long, 0.5-0.7 mm. broad, white to lilac. *Fruit* 1.5-2 mm. long, 0.5-0.7 mm. broad, linear-cuneate, flat, the body black, with slightly thickened straw-coloured smooth margins, and sometimes with a few curled hairs on the central area. Pappus microscopic.

Key to varieties.

- (1). Leaves entire or rarely with 1-3 small teeth, up to 3.2 cm. long var. *α parvula*.
 (1)*. Leaves pinnatisect, up to 10 cm. long with 3-5 segments var. *β lissocarpa*.

Brachycome parvula Hook. f., var. *α parvula* comb. et stat. nov.

(Text-figs. 87, 99; Plate vi, map 26.)

Synonymy: *B. parvula* var. *α* Hook. f., Fl. Tas., 1 (1860), 185. *B. parvula* var. *β* Hook. f., ibid. *B. graminea* var. *angustissima* Sond., Linnaea, xxv (1852), 478. *B. graminea* var. *heterophylla* Sond., ibid.

Haptotype: *Killicrankie, Boat Harbour, N.E. of Flinders Island, 23.11.1884, Dr. Milligan (MEL).

Perennial glabrous herbs up to 15 cm. high, frequently branching from the base. Stolons noted on several specimens. Leaves radical and cauline, or cauline only on larger specimens. Cauline leaves usually numerous, sessile, entire, obtuse, linear or oblanceolate, the lower rarely with 1-3 small teeth. *Peduncles* leafy proximally. *Capitula* up to 40. *Ray florets* about 40.

Habitat: Typically coastal, frequently found under saline and subsaline conditions.

Range: Mainly southern portions of Victoria and coast of Flinders Island.

Specimens examined:

Victoria: Snowy R., 11.1904, C. H. Grove (NSW); Cunningham, 1.1911, H. B. Williamson (MEL); Sandringham, south of Red Bluff, "high sea cliffs", 2.1945, J. H. Willis (MEL); Dandenong Ranges, 1.1853, F. Mueller (MEL); Brighton, "grassy meadows, rays white", 1.1853, F. Mueller (MEL); *Brighton, 5.1896, C.M. (NSW); Yarra, 1853, F. Mueller (NSW); Yarra, F. Mueller (lectotype of *B. graminea* var. *angustissima*, HARVARD); Yarra, "Saline and subsaline pastures", 1.1853, F. Mueller (MEL); Mt. William, "Flats", 4.1872, D. Sullivan (MEL); Port Phillip, "Saline pastures", F. Mueller (MEL); Port Phillip, F. Mueller (MEL); Mordialloc, Pt. Phillip Bay, "Saline marshy ground near the sea", 22.12.1899, W. R. Baker (MEL); Little River, near Station Peak, Geelong, F. Mueller (MEL); Warnambool, 12.01, H. B. Williamson (NSW); Warnambool, "Cliffs", 4.08, — Roberts (MEL); *Gorae West, near Portland, 12.44, C. Beauglehole (MEL); Wannon R., 11.1900, H. B. Williamson (NSW).

Flinders Island: *Killicrankie, Boat Harbour, N.E. of Flinders Island, 23.11.1844, Dr. Milligan (haptotype of var. α Hook, f., MEL); sea coast, wet plains, 2.11.1845, Dr. Milligan (haptotype of var. β Hook, f., MEL).

South Australia: Lake Alexandrina, "margin", 4.1848, F. Mueller (MEL); *edge of Bunda Cliffs, 15.2.1879, R. Tate (AD, MEL).

Tasmania: Gordon River, 14.12.1846, J. Milligan (HO); "Tasmania", W. H. Archer (NSW).

Hooker based his description of this species on a small series of specimens collected by Milligan from Flinders Island. He divided these specimens into two varieties, α and β , based on differences in habit such as height, and number of stems present. Examination of a larger series shows that these characters are environmental ones, and not varietal criteria, so the varieties are accordingly not confirmed, and are grouped together under *B. parvula* var. *parvula*. A specimen in the National Herbarium, Melbourne, which bears the type data, was selected as haptotype for the species, and therefore of var. *parvula*, as it is uncertain whether Hooker ever handled this particular specimen.

This variety is almost entirely confined to Victoria, where it is found mainly in the coastal belt. The record from Bunda Cliffs suggests that further collecting may produce specimens between this locality and Lake Alexandrina.

Variation within the variety is slight and though individual leaves sometimes depart from the typical entire condition, there are always sufficient of the normal leaves for the plant to retain its characteristic appearance.

The fruits are quite distinct from those of any other species, but are closest to those of *B. Tatei*.

Brachycome parvula var. β *lissocarpa* (J. M. Black) comb. nov.

(Text-fig. 88; Plate vi, map 26.)

Synonymy: *B. lissocarpa* J. M. Black, *Proc. Roy. Soc. S.A.*, lii (1928), 227.

Lectotype: Yallum, south-east S.A., J. M. Black (MEL).

Lectoparatypes: Two, l.c. (JMB, AD).

Weakly erect branching (?) annuals, more or less glandular distally. Leaves radical and cauline, pinnatisect, up to 10 cm. long, the segments 3–5, up to 1.1 cm. long, 1.2 mm. broad, linear, sub-acute. *Peduncles* naked or with 1 or 2 bracts proximally. *Capitula* about 4. *Ray florets* up to 80.

Habitat: Sheltered places, chiefly in gullies.

Range: Western Victorian to eastern South Australia.

Specimens examined:

Victoria: Victorian Ranges, "rocky places", 11.1853, F. Mueller (MEL); Victorian Ranges, "Moist declivities", (?) F. Mueller (MEL); Upper Wannon R., 9.11.1903, H. B. Williamson (MEL); Wannon Valley, Grampians, 11.1903, H. B. Williamson (MEL); Grampians, 11.1903, H. B. Williamson (BRI); Mt. Sturgeon, F. Mueller (lectotype of *B. graminea* var. *heterophylla* MEL; lectoparatype HARVARD); Glenelg, F. Mueller (MEL).

South Australia: St. Vincent's Gulf, F. Mueller (MEL); Blumberg, 26.10.1881, R. Tate (AD, JMB); Golden Grove at Blumberg, 1881, R. Tate (JMB); Blumberg, 30.9.1881, R. Tate (AD); Head of Scott's Creek, 9.11.1885 (JMB); Lofty Ranges, "valleys", F. Mueller (MEL); Coromandel Valley, 1894, J. G. O. Tepper (JMB); Tintaro, 9.10.1881, R. Tate (AD); Port Elliott, Hussey (AD); Myponga, 13.10.1926, J. B. Cleland (JBC); Myponga, 21.10.1932, J. B. Cleland (JBC); *Back Valley off Inman Valley, 13.9.1925, J. B. Cleland (JBC); Back Valley, 15.9.1935, J. B. Cleland (JBC); *Inman Valley near Encounter Bay, 15.9.1925, J. B. Cleland (JMB); Victor Harbour, 10.1911, McErroy (JMB); Yallum, J. M. Black (lectotype, MEL; lectoparatypes, JMB, AD); Yallum, 10.1905, J. M.



Black (NSW); Mt. Graham, 20.11.1872, R. Tate, "fern brakes" (AD); Happy Valley, 9.10.1935 (AD); St. Vincent's Gulf, F. Mueller (MEL); Ewen's Ponds, Pt. MacDonnell, 30.10.1941, J. B. Cleland (JBC).

Fruit of *B. lissocarpa* being identical in every way with those of *B. parvula*, the former species has been reduced in status without change of epithet. No significant variation was noted in the series examined. The geographical distribution of these two varieties is interesting in that one can be said to begin where the other leaves off, there being a slight overlap in western Victoria.

41. BRACHYCOME BELLIDIOIDES Steetz. Pl. Preiss, i (1845), 426.

(Text-figs. 89, 100; Plate vi, map 27.)

Lectotype: "In clayey borders of woods above the town of Perth." Preiss No. 99. "Received" 1843 (MEL).

Lectoparatypes: Five, l.c. (MEL).

Erect glabrous annuals up to 13 cm. high, with one to several stems arising basally, and terminating in a slender peduncle. *Leaves* entire or with one to three small lateral teeth, linear to broad linear, sessile, obtuse to sub-acute. Radical leaves forming a basal cluster up to 1 cm. long, 1.3 mm. broad. *Peduncles* filiform. *Capitula* 1-9, usually 1-3, about 7 mm. diameter. *Involucral bracts* about 28, 2.3-2 mm. long, 0.7-1.2 mm. broad, ovate, subacute to acute, entire or slightly serrulate. *Ray florets* up to 26, rays about 6 mm. long, 1.2-2.3 mm. broad, white. *Receptacle* convex to broadly conical, 1.5-2.5 mm. broad, 0.8-1.2 mm. high, very slightly pitted. *Fruit* 0.9-1.1 mm. long, 0.5-0.6 mm. broad, black with minute rectangular papillae, giving the fruit a microscopic tessellated appearance, flattened, cuneate, glabrous, smooth or tetragonal. Pappus coroniform, minute.

Range: Mainly south-western coastal district of Western Australia.

Specimens examined: Victoria Springs, 1891, R. Helms (MEL); Guildford, 4.9.1901, C. Andrews, "Sand" (PERTH); *W. A. Oldfield (PERTH); Bellevue, near Perth, 10.1943, Consett Davis (NSW); "In clayey borders of woods above the town of Perth, received 1843", L. Preiss, n. 99 (lectotype and lectoparatypes, MEL); Fremantle, 8.1900, W. V. Fitzgerald (NSW); W.A., 1902, A. G. Hamilton (NSW); King George's Sound, 10.1901, B. T. Goadby (NSW).

In the original description Steetz quotes the type locality as "In the clayey borders of woods above the town of Perth, l.ix.1839, Herb. Preiss, n. 99". A sheet of mounted specimens has been examined which bears the determination "*Brachycome bellidioides nobis*" and bears the type data in Steetz's handwriting. The date of collecting is not recorded on the sheet, although it is noted in the description, but the record "emi 1843" is taken to indicate the date of receipt of these specimens by Steetz. Since this predates that of the publication of the name there is no doubt that these specimens form at least part of the syntype series, and from them lectotype and lectoparatype selection has been made.

This species is vegetatively indistinguishable from *B. pusilla*, except for the colour of the ray florets (a doubtful criterion), which is doubtless the reason Bentham (1866) listed it as a synonym of that species. It is interesting to note that in his original description of *B. pusilla*, Steetz makes the comment "examined superficially the plant belongs to *B. bellidioides*, but the fruits of the two species are exceedingly different". Steetz's opinion is now confirmed, and *B. bellidioides* is reinstated as a valid species. Since the fruit develops its typical characters at an early stage, determination is seldom in doubt.

This species can best be regarded as having sprung from the *B. iberidifolia* stock, with which certain similarities in the fruit are apparent. The microscopically tessellated appearance of the fruit of both species is a striking character in common, which, with the same size, general shape, and small pappus, indicates a close relationship. The

Text-figures 89-96. Habit studies. $\times \frac{1}{2}$.

- 89, *B. bellidioides* (Lectoparatype). 90, *B. pusilla* (Lectotype). 91, *B. exilis*.
 92, *B. trachycarpa* (Lectotype). 93, *B. rigidula* (Lectotype of *B. multicaulis*).
 94, *B. ciliaris* var. *lanuginosa* (Lectotype). 95, *B. ciliaris* var. *lyrifolia*.
 96, *B. ciliaris* var. *subintegrifolia* (Holotype).

glabrous nature of the fruit of *B. bellidioides* and their smooth or somewhat tetragonal outline make them readily distinguishable from the centrally depressed fruit of *B. iberidifolia*.

42. BRACHYCOME PUSILLA Steetz. Pl. Preiss, i (1845), 426.

(Text-figs. 90, 101; Plate vi, map 27.)

Lectotype: Near Helena River, W.A., Dr. Preiss, No. 86, "received 1843" (MEL).

Lectoparatypes: Six, l.c. (MEL).

Slender, erect, glabrous annuals, up to 11.3 cm. high, branching from the base, each stem terminating in a filiform peduncle. Leaves radical and cauline, simple, entire, linear to broad linear, sub-acute. Radical leaves in a basal cluster, about 7, occasionally with 1-2 minute teeth, up to 1.7 cm. long, 1 mm. broad, the basal pair connate. Cauline leaves up to 1.2 mm. long, 0.8 mm. broad. *Capitula* 1-2, 5 mm. diameter. *Involucral bracts* about 14, 2.5 mm. long, 1.2 mm. broad, sub-acute to acute, slightly torn-ciliate. *Ray florets* about 14, the rays 2.5-4 mm. long, blue. *Receptacle* broadly conical, about 1 mm. broad, 0.5 mm. high. *Fruit* brown, 1.8 mm. long, 0.9 mm. broad, narrow cuneate, flattened, with a longitudinally depressed area on each face, surrounded by a thick smooth margin. Long apically rolled hairs are scattered over the fruit, particularly at the summit. Pappus minute, coroniform.

Range: South-western coastal region of Western Australia.

Specimens examined: Near Helena River, Swan River Colony, "Received 1843", Dr. Preiss, No. 86 (lectotype and lectoparatypes, MEL); "In calcareous gully not far from the town of Fremantle", "received 1843", Dr. Preiss, No. 98 (MEL); Wooroloo, 9.1916, F. Stoward (PERTH); Claremont, 9.1901, W. V. Fitzgerald (NSW); W.A., 1902, A. G. Hamilton (NSW).

The same method of type selection as indicated for *B. bellidioides* was used in this instance. The syntype specimens are affixed to a sheet with the determination "*Brachycome pusilla nobis*" in Steetz's writing, and bear the same number (Herb., Preiss, No. 86) as is quoted by Steetz.

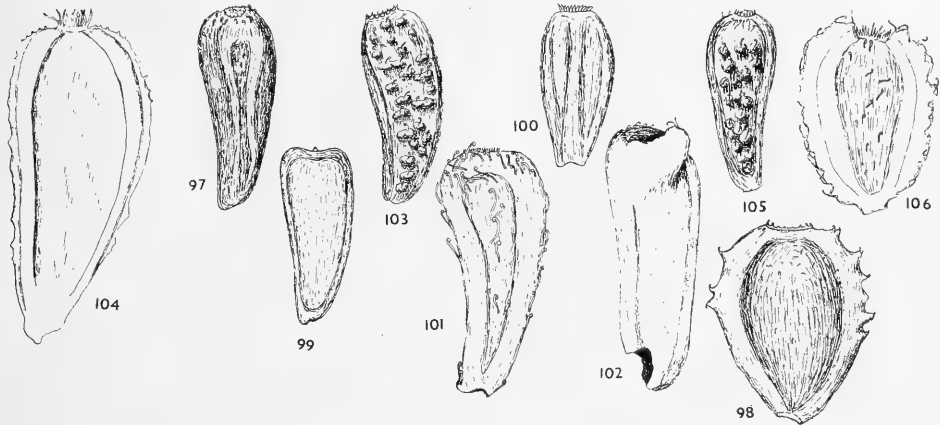
This species is remarkably constant in all characters, and variation is limited to small differences in size of the plant itself and of its parts. Where several stems are present, the central one is upright and the remainder ascending. No evidence has been found to support Bentham's statement that the fruit are dimorphic. Occasionally a small tooth can be found on the radical leaves.

As already noted, this species is vegetatively identical with *B. bellidioides*, but the constant presence of curled hairs on even extremely young fruit makes diagnosis certain long before maturity is attained.

B. pusilla is very closely related to *B. iberidifolia*, both species being frequently found in the same locality, though the former appears to have a more restricted range. Vegetatively there is little similarity between the species, *B. iberidifolia* being easily recognized by its large size and much branched stem bearing pinnatisect leaves, while in *B. pusilla* the stem frequently branches from the base, and although a few cauline leaves are present, most leaves are radical, and both kinds are entire. A few specimens of *B. iberidifolia*, however, have been examined which bear leaves which are entire or mostly so, and in the case of *B. pusilla* a few teeth or short lobes can sometimes be found on the radical leaves. Certain similarities are apparent in the fruit of both species, the presence of curled hairs chiefly towards the summit being the most striking. Usually two shallow longitudinal ridges can be seen on the fruit of *B. iberidifolia*, and it is frequently distended distally so that the minute pappus cannot be seen in lateral view. In this respect there is an approach to the shouldered type of fruit typical of *B. exilis* Sond., and it is possible that that species originated as a geographic sub-species of *B. iberidifolia*; in this connection the present range of the two species is interesting. The fruit of *B. pusilla* can be readily distinguished from those of *B. iberidifolia* by their relative smallness, and the fact that they do not possess the microscopic tessellations characteristic of the latter species. In addition to these characters, the fruit of *B. pusilla*, in the specimens examined, are obovate and bear a thickened margin.

43. BRACHYCOME EXILIS Sond. *Linnaea* xxv (1852), 449.

(Text-figs. 91, 102; Plates vi, map 28; xiii.)

Synonymy: *B. exilis*, var. *scabrada* Benth, Fl. Aust., iii (1866), 516. *B. neglecta* J. M. Black, Proc. Roy. Soc. S.A., lii (1928), 228.*Lectotype*: Fielder's Section, Adelaide, Dr. Behr (Gray Herbarium, HARVARD, ex herb, W. Sonder).Text-figures 97-106. Fruits. $\times 17$ approx.

97, *B. iberidifolia*. 98, *B. Tatei*. 99, *B. parvula*. 100, *B. bellidioides*. 101, *B. pusilla*.
 102, *B. exilis*. 103, *B. trachycarpa*. 104, *B. rigidula*. 105, *B. ciliaris*. Ray fruit.
 106, *B. ciliaris*. Disc fruit.

Erect or straggling plants, up to 18 cm. high, glandular pubescent distally. Radical leaves 1-4 cm. long, entire or pinnatisect, the segments up to 3 mm. long, 0.5 mm. broad, acute. Cauline leaves sessile, pinnatisect, up to 2 cm. long, with lobes up to 5.5 mm. long, 0.9 mm. broad, sub-acute, linear, occasionally toothed. *Peduncles* naked. *Capitula* 1 to about 40, 4-6 mm. diameter. *Involucral bracts* 10-18, 1.5-3.2 mm. long, 0.5-1.2 mm. broad, obtuse to sub-acute, oblanceolate, entire. *Ray florets* 17-20, the rays about 3 mm. long, 1 mm. broad, white. *Receptacle* 1 mm. broad, 0.3 mm. high, slightly convex, not pitted. *Fruit* clavate, tetragonal, shouldered distally, slightly compressed below, 1.5-2 mm. long, 0.5 mm. broad distally; hairs at the summit incurved, a few short ones sometimes on the lateral margins. Pappus absent. Fruit reflexed on receptacle at maturity.

Habitat: Several of the larger specimens bear a collector's note "in scrub", while some of the smaller ones were entangled with specimens of *B. leptocarpa* or *B. gonocarpa*, which suggests a moist or swampy habitat with short grass.

Range: South-western New South Wales, western Victoria, South Australia as far north as Hawker.

Specimens examined:

New South Wales: Lachlan R., 9.1878, F. Mueller (MEL); near R. Darling, 28.10.1860, Vic. Expl. Exped. (MEL); across R. Murray, "desert", D. Schulzen (?), 1848 (lectotype, *B. exilis* var. *scabrada* Benth., MEL).

Victoria: Wimmera, Dallachy (MEL, NSW).

South Australia: Near Hawker, plain, 4.10.06, 21.10.16, J. M. Black (JMB); Corona, Iron Knob, 6.85, W. L. Cleland (JBC); Telowie Gorge, 21.9.1906, J. M. Black (JMB); Pt. Pirie, 23.9.1906, J. M. Black (JMB); *West Coast, Richards (AD); Streaky Bay, Warburton (MEL); between Pt. Lincoln and Streaky Bay, 10.1882, A. Richards (AD); Port Lincoln district, 11.1887, R. Tate (AD); Port Lincoln district, F. Mueller (MEL); S.Y.P., 11.1889, R. Tate (AD); Clarendon, near Mt. Lofty, O. Tepper (MEL); McLaren Vale, 1.11.1883, "Scrub", M. A. Aldersey (MEL); *Patawalonga, 1.10.1883, R. Tate (AD); Hallet's Cove, 1928, J. B. Cleland (JBC); Holdfast Bay, "Sandhills", 27.10.1881 (AD); Mt. Barker, 29.9.1848, F. Mueller (MEL); Strathalbyn, *2.10.1906, J. M. Black (JMB); Strathalbyn, 25.9.1909, "Scrub" (lectotype, *B. neglecta*, JMB; lectoparatype, MEL); Kinchinda, 10.1926, J. B. Cleland (JBC, JMB); Kinchinda, 17.9.1927, J. B. Cleland (JBC); *between Murray Bridge and Callington, "scrub" (JMB); Murray Bridge, "margins of lagoons, etc.", 27.11.1887, O. Tepper, n. 33 (MEL); east of Wellington, "scrub", R. Tate (AD, MEL); Blackford, near Kingston, 6.3.1941, J. B. Cleland (JBC); Caneka, 25.11.1882,

R. Tate (AD); Mosquito Creek, 25.11.1882, R. Tate (AD); Edwards R., 10.1875, F. Mueller (MEL); Barossa Ra., 10.1848, F. Mueller (MEL); Althorpes, 9.1907, R. S. Rogers (NSW).

Western Australia: Israelite Bay, 1885, Brooke (MEL).

A considerable amount of confusion has hitherto existed with regard to the identity of this species. A specimen in the National Herbarium, Melbourne, from the summit of Mt. Barker, one of the type localities quoted by Sonder, has been used as a basis of comparison. There is no evidence that Sonder handled this particular specimen, it probably being a duplicate of one sent to him by Mueller. The author is indebted to Miss Bernice G. Schubert of the Gray Herbarium, Harvard University, for a photograph of one of the syntypes of this species (Fielder's Section, Adelaide, Dr. Behr) from Sonder's Herbarium, and loose fruit from this specimen. Both vegetative features and details of the fruit confirm the view that these two specimens are conspecific, and the one from Harvard has been selected as lectotype of the species.

When Bentham redescribed *B. exilis* in *Flora Australiensis* (iii, 1866) he had before him specimens of *B. leptocarpa* F. Muell., of which he gives an accurate description. He lists *B. leptocarpa* as a synonym and he quotes a number of specimens which have been traced and identified as that species. This mistake has been repeated in all subsequent Australian Floras, with the result that all specimens of *B. leptocarpa* have been identified as *B. exilis*. At the same time there existed a moderately common species in western Victoria and South Australia which was not described in any flora. This fact was recognized by Black who, in 1928, described *B. neglecta*. Syntype material of this latter species has been examined and a lectotype selected, which is conspecific with *B. exilis*. The name *B. neglecta* is consequently a synonym of *B. exilis*, and the latter species has been redescribed in its original (Sonder's) sense.

The var. *scabrída* described by Sonder was founded on a specimen collected by Dr. Schulzen, "in desert, on other side of Murray River", a haptotype of which has been nominated. This specimen is considerably larger in all vegetative features than the type material of *B. exilis*, but differs in no essential manner. The herbarium specimens in Australia of this species show a continuous and relatively wide range of variation, and it is suggested that Sonder's specimens of *B. exilis* and that of var. *scabrída* represent the limits of intra-specific variation. Since the differences shown by var. *scabrída* are of degree rather than of nature, this variety has been rejected.

Variation within this species is confined to vegetative features, none of which are sufficient to warrant varietal status. Although typically the leaves are pinnatisect with linear lobes confined to the distal portion of the blade, a specimen was noted from Wellington, S.A., in which the lobes are closely approximated to the stem, and some of the upper leaves are palmate in outline.

The small amount of variation noted in the fruit is confined to the degree of swelling distally, and the number of curled hairs present, the former increasing, and the latter decreasing with maturity.

One specimen, from Clarendon, is interesting in that the fruits are densely covered with papillae, but until further specimens are available showing this character, the variation is merely recorded.

B. exilis is related to *B. iberidifolia*, both in vegetative features and fruit structure, though both species are quite distinct. Many fruits of *B. iberidifolia* are slightly swollen distally, and all bear curled hairs, which suggests that *B. exilis* and *B. iberidifolia* may have originated as geographic sub-species, a view which is supported by the present distribution of these two species.

8. Superspecies TRACHYCARPA.

44. BRACHYCOME TRACHYCARPA F. Muell. *Linnaea* xxv (1852), 339.

(Text-figs. 92, 103; Plate vi, map 28.)

Lectotype: Crystal Brook, S.A., 10.1851, F. Mueller (MEL).

Lectoparatype: *l.c. (MEL).

Branching erect plants, probably perennial, 10-40 cm. high, with glandular-scarbid stems. Leaves cauline, sessile, glabrous, broad linear, sometimes canaliculate, frequently

basally crowded. Lower leaves sub-acute to acute, 1-3.5 cm. long, 1.5 mm. broad, frequently with 2-4 smaller leaves arising from the axils, entire or pinnatisect with 1-6 acute, narrow-linear lateral lobes 3.5-6 mm. long, 0.7-1 mm. broad. Upper leaves 2-3 mm. long, 0.5-0.7 mm. broad, acute, or with 1-3 filiform lobes. Young leaves usually slightly glandular. *Peduncles* naked or with a solitary median bract. *Capitula* up to 10, 4-5 mm. diameter. *Involucral bracts* 12-19, 2-2.3 mm. long, 0.7-1.1 mm. broad, oblong-cuneate, sub-acute with torn ciliate margins, minutely glandular on the outer surface. *Receptacle* convex, slightly pitted, 1-1.2 mm. broad, 0.8 mm. high. *Ray florets* 13-14, the rays 5 mm. long, 1.1 mm. broad, "lilac". *Fruit* narrow-oblong-cuneate, brown, 1.5-1.8 mm. long, 0.6-0.8 mm. broad, flattened, tuberculate on the centre of each face, each tubercle bearing a few small glandular hairs; margin smooth. Pappus minute, crown-shaped.

Habitat: Pasture-land and open forest.

Range: Southern Queensland, through western plains of New South Wales, and western Victoria to southern districts of South Australia.

Specimens examined:

Queensland: Mitchell District, "in grassland on dark greenish-brown caly", 1,100', 3.5.1934, S. T. Blake (BRI); Mungallala, "brown loam, amongst grasses. Rays lilac", 1,390', C. E. Hubbard, n. 6038 (BRI); Roma, B. Scortechini (BRI); Dulacca, 3.1909, J. H. Maiden (NSW); between Miles and Chinchilla, 31.5.1946, C. T. White (BRI); Chinchilla, 1.1931, R. C. Beasley, n. 45 (BRI); Kindon, 54 miles NNE of Goondiwindi, 7.12.1938, L. S. Smith, n. 602 (BRI).

New South Wales: Boggabilla, "Sandy soil in rung forest", 1.1935, C. W. Winders (BRI); head of the Gwydir, Liverpool plains, L. Leichhardt (MEL); *Warren, 3.1909, J. H. Maiden (NSW); Darling R., Dallachy (MEL).

Victoria: Dimboola, 2.5.1892, F. M. Reader (MEL).

South Australia: Leister, 80 miles N. of Ooldea, "Sandhills", W. H. Tietkins (AD); Ooldea, 3.1921, Bates (JMB); Tarcoola, "violet", 19.9.1920, J. M. Black (JMB); 8 miles W. of Koonibba, 22.8.1928, J. B. Cleland (JBC); Koonibba, 19.8.1928, J. B. Cleland (JBC, JMB); Murat and Denial Bays, 9.1907, R. S. Rogers (NSW); Thevenard Penin., 1926, E. Pearce (JMB); West Coast, Richards (AD); Gawler Ra., 9.1912 (JMB); Nonning, 5.1931, Pulleine (JMB); Mt. Brown, 13.11.1881, R. Tate (AD); Crystal Brook, 10.1851, F. Mueller (lectotype and lectoparatype, MEL); Cundaka, 10.1851, F. Mueller (MEL, NSW); Mannum, 5.1931, Pulleine (JBC).

Variation within this species is limited to the leaves, which are either entire or pinnatisect. The tuberculate nature of the fruit is not apparent when immature, but the position of the future tubercles is marked by short glandular hairs.

45. BRACHYCOME RIGIDULA (DC) comb. nov.

(Text-figs. 93, 104; Plate vi, map 28; xi, 1.)

Synonymy: *Steiroglossa rigidula* DC., Prod. vi (1838), 39. *B. strongylopermoides* Walp., Linnaea, xiv (1840), 305. *B. squalida* Hook. f., Lond. Journ. Bot., vi (1847), 115. *B. multicaulis* F. Muell., Trans. Phil. Soc. Vic., 1 (1855), 43. *B. ciliaris* (Labill.) Less., var. *robusta* Benth., Fl. Aust., iii (1866), 519.

Lectotype: No. 8, "A pretty blue flowering plant, rare in loamy damp plains on the south of Lake George, N.S.W., lat. 35° 4', April, 1824", A. Cunningham (GENEVA).

Haptotypes: Lake George, 4.1824, A. Cunningham (MEL, BRI).

Many stemmed branching perennials, erect or ascending, up to 36 cm. high. Stems glandular hairy, densely leafy proximally. Leaves cauline, up to 1.8 cm. long, pinnatisect, crowded, the segments narrow-linear to linear, pungent-pointed, up to 8 mm. long, 1.1 mm. broad. *Peduncles* terminating branches, glandular, usually with a single entire small leaf about the middle. *Capitula* up to 30, 8-10 mm. diameter. *Involucral bracts* about 20, up to 5 mm. long, 1-1.5 mm. broad, oblong, obtuse, with torn ciliate margins. *Receptacle* conical, 1.2 mm. broad, 1 mm. high. *Ray florets* up to 40, "blue", the rays 8 mm. long, 1.3 mm. broad. *Fruit* 2.2-2.9 mm. long, 1-1.5 mm. broad, obovate, flat, light to dark brown, body with an entire or irregularly dissected narrow straw-coloured wing. Pappus usually conspicuous.

Habitat: Well-drained situations among rocks at high elevations.

Range: Southern Queensland and highlands of New South Wales, from Wallerawang through the Southern Alps to the Grampians in Victoria. Also found in Tasmania.

Specimens examined:

Queensland: Stanthorpe, 12.75, F. M. Bailey (BRI).

- New South Wales*: Sunny Corner, 1.1885, E. Betche (NSW); Wallerawang, 11.1899, J. H. Maiden (NSW); Badgery's Crossing, Shoalhaven R., 25 miles W. of Nowra, 8.10.1945, F. A. Rodway (NSW); Lake George, 4.1824, A. Cunningham, n. 25 (haptotypes, MEL, BRI); Lake George, 4.1824, A. Cunningham, n. 8 (lectotype, GENEVA); Queanbeyan, "Ray flowers blue", 1.1888, E. Betche (NSW); Braidwood district, 3,100', 12.1884, W. Bauerlen, n. 263 (MEL); Kiandra district, "top of Mt. Tabletop, 6,000'", 2.1897, E. Betche (NSW, BRI); Ettrema, sides of canyon, 5.1.1947, F. A. Rodway (NSW, BRI); Talbingo-Adaminaby Road, <3,000', 4.12.1943, S. Copland (NSW, BRI); Cooma, 12.1890, E. Betche (NSW); Cooma, 8.2.1908, R. H. Cambage, n. 1832 (NSW); Bombala district, 2-3.1885, W. Bauerlen, n. 15 (MEL); Bombala, 12.1886, W. Bauerlen, n. 291 (MEL); Bombala, 12.1896, J. H. Maiden (NSW).
- Victoria*: Murray R., F. Mueller (MEL); Australian Alps, F. Mueller (MEL); *Buffalo Mts., 1906, H. B. Williamson (MEL); Mt. Hotham, 1.1899, C. Walter (NSW); Mt. Hotham, 1.1900, J. H. Maiden (NSW); Mt. Hotham, 28.3.1936, R. A. Black (RAB); near Omeo, "on open ranges, 2,000'-3,000'", 1883, J. Stirling (MEL); Swift's Creek, "On stony hillsides, 1,600'-2,000'", 10.1944, W. Hunter (MEL); Mt. Buller, "on the rocky summit", 23.3.1853, F. Mueller (lectotype and lectoparatype of *B. multicaulis* and *B. ciliaris* var. *robusta*, MEL, NSW); Mt. Buller, 5,000', 3.1853, F. Mueller (MEL); Mt. Buller, "on the highest rocky declivities", 3.1853, F. Mueller (MEL); Mt. Ligar, 4,000', 1.1859, F. Mueller (MEL); East Gippsland, E. F. Fricke (AD); Hall's Gap, Grampians, 12.1899, H. B. Williamson (MEL).
- Tasmania*: Top of Spring Hill, 22.3.1842, Gunn, n. 708 (NSW); Swansea, L. Rodway (HO); Grindelwold, 18.2.1845, Gunn, n. 706 (NSW); Tasmania, Archer (NSW); Tasmania, Storey (MEL).

The author is indebted to Professor Baehni of Geneva for a floret, young fruit and photograph of De Candolle's specimen of *Steiroglossa rigidula*, which leave no doubt as to the identity of this species. Specimens matching that of De Candolle and also collected at Lake George in April, 1824, by Cunningham have been found at the National Herbarium, Melbourne, and the Brisbane Herbarium. These specimens have been used as a basis of comparison for all others examined. Syntype material of *B. multicaulis* F. Muell. and *B. ciliaris* var. *robusta* Benth., is identical and lectotype and lectoparatype have been selected though the epithets are abandoned as later synonyms. Attempts to trace any of Walper's specimens of *B. strongylospermoides* ("New Holland. Lhotsky") have been unsuccessful, but his description agrees satisfactorily with *B. rigidula*, and until definite proof to the contrary is forthcoming, the synonymy given by Bentham (1866) is adopted. Syntype material of *B. squalida* Hook. f. ("Spring Hill, Gunn") is at Kew, but there is a specimen in the National Herbarium, Sydney, from Gunn's personal collection which bears the type caption. It is probable that this specimen is a merotype, though there is no means of establishing this fact.

In his description of *B. multicaulis*, Mueller describes dimorphic fruit, those of the disc bearing narrower wings than those of the ray florets. Dissection of a large number of capitula with mature fruits has failed to confirm this observation but has shown that a large percentage of inner fruit abort, and it was doubtless these aborted or undeveloped fruit which Mueller described as typical of the disc florets.

B. rigidula is most closely allied to *B. ciliaris* (Labill.) Less., in which species it was incorporated by Bentham as var. *robusta*. The fruits are similar to those of the disc of *B. ciliaris*, but as the typical ray fruits of that species do not occur, it has been reinstated as a full and valid species. It is suggested that it was from *B. rigidula* that *B. ciliaris* evolved, by the development of dimorphic fruit. In that connection the range of *B. rigidula* is interesting, being confined as it is to high elevations, and although wide areas exist between some of the regions, in which this species does not occur, there is no significant variation between specimens from widely separated localities. This implies that in former times the species occupied a wide range in eastern Australia, but was ultimately displaced over most of it by its subspecies, our present *B. ciliaris*. Evolution seems to have been accompanied by a westerly spread of the *B. ciliaris* population which ultimately reached Western Australia, while *B. rigidula* became confined to high elevations, the intervening low areas constituting natural barriers to its migration.

46. BRACHYCOME CILIARIS (Labill.) Less. Syn. Comp. 192, 1832.

Much branched erect or ascending perennials, up to 44 cm. high, more or less shortly glandular-pubescent or sparsely to densely covered with woolly white hairs.

Leaves cauline, up to 6 cm. long, linear to lyrate; entire, pinnatisect or lyrate. Lobes, when present, acute to pungent-pointed, narrow to broad-linear, entire or rarely with a single lateral tooth. *Peduncles* leafy proximally. *Capitula* 1–200, 4–10 mm. diameter. *Involucral bracts* 12–30, 2–4.5 mm. long, 0.6–1.5 mm. broad, lanceolate to narrow obovate, usually more or less glandular, sub-acute to acute with torn-ciliate margins. *Ray florets* 20–55, the rays, 2.5–7 mm. long, 0.5–1 mm. broad, white to purple. *Receptacle* 1.1–2.4 mm. broad, 0.9–2 mm. high, steeply convex to conical, slightly to moderately pitted. *Fruit* dimorphic. *Ray fruit* 1.3–1.8 mm. long, 0.4–0.7 mm. broad, dark brown to black, oblong-cuneate, flattened, tuberculate on each face, with a few glandular hairs, the margins smooth. Pappus microscopic to minute. *Disc fruit* 1.5–2.5 mm. long, 0.8–1.5 mm. broad, obovate, the body flattened, elliptical, brown to black, glabrous or with a few curled glandular hairs, marginally winged; wing white or straw-coloured, entire or irregularly and shallowly lobed with relatively long curled glandular hairs on the margin. Pappus relatively conspicuous and at least equal to the apical notch between the wings, or minute, always larger in the disc fruit than in the ray fruit of the same head.

Key to the varieties.

1. Leaves pinnatisect or pinnatifid 2
2. Stems bearing long white woolly hairs var. *β lanuginosa*
- 2.* No such indumentum present 3
3. Leaves usually pinnatisect with linear segments var. *α ciliaris*
- 3.* Leaves lyrate or more or less obovate and irregularly toothed var. *γ lyrifolia*
- 1.* Leaves mostly entire var. *δ subintegrifolia*

Brachycome ciliaris (Labill.) Less., var. *α ciliaris*, comb. et stat. nov.

(Text-figs. 105, 106; Plates vi, map 29; xi, 2.)

Synonymy: *Bellis ciliaris* Labill., Pl. Nov. Holl., ii (1806), 56. *Brachycome Drummondii* Walp., Rep. ii (1843), 584. *B. ciliaris*, var. *glandulosa* Benth., Fl. Aust., iii (1866), 519. *B. ciliaris*, var. *grandiflora* Benth., *ibid.* *B. ciliaris*, var. *subdissecta* Benth., *ibid.*

Lectotype: *New Holland, 1806, J. J. Labillardière (PARIS).

Peduncles, *involucral bracts* and young leaves, more or less glandular-pubescent, rarely glabrous. Leaves pinnatisect, the lobes occasionally reduced to teeth, rarely double pinnatisect. Lobes 3–9, up to 1.6 cm. long, 2 mm. broad, pungent pointed, narrow to broad linear.

Habitat: Apparently rather dry, well-drained situations.

Range: Unrecorded from Queensland except for a single flowering specimen and another, the locality of which has not been traced. Southern highlands and western districts of N.S.W., western Victoria.

Specimens examined:

Queensland: *N.N.W. Bungunya, Darling Downs, "in Brigalow-belah scrub on compact brown soil, about 700 ft. Pale green rosettes. Ray lilac, disc yellow", 26.7.45, S. T. Blake (BRI); Mally Station, 5.1919, J. L. Watts (BRI).

New South Wales: Morden, 17.8.1883, MacGillivray (NSW); Broken Hill and Torrowangee, 8.1892, H. Deane (NSW); Stephen's Creek, Broken Hill, 7.8.1921, A. Morris (NSW); South Ita, 19.9.1925, A. Morris (NSW); Moorkai Hills, 23.10.1921, A. Morris (NSW); Cobar, 8.1911, L. Abrahams (NSW); Cooma, 12.1896, J. H. Maiden (NSW).

Victoria: Murray R., at Echuca, 10.1886, H. King (MEL); Brentwood, 11.1901, S. P. Croom (NSW); Shire of Dimboola, 30.9.1891, 9.10.1894, F. M. Reader (MEL); north-west of Horsham (MEL); Horsham, 11.1901, S. P. Croom (BRI); Wimmera district, Dallachy (MEL, NSW); Wimmera, 10.1900, C. Walter (NSW); Borung "Pastures", 19.1.1903, F. M. Reader (MEL); Forest Crk., near Castlemaine, 12.1852, F. Mueller (MEL).

Central Australia: Osborne Ranges, "Rocky Hill, Quartzite", 7.1922, C. E. F. Allen (NSW); Finke R., 17.5.1894, R. Tate (JMB).

South Australia: Lambina, 21.8.1933, J. B. Cleland (JBC); Mt. Lyndhurst, Flinders Range, 9.1898, M. Koch (AD); Wilpena pound, 10.11.1930, J. B. Cleland (JBC); Wilpena pound, 10.1939 (AD); Koonamore, 19.8.1931, T. B. Paltridge (AD); Port Augusta, 1.9.1944, J. B. Cleland (JBC); Crystal Brook, 10.1851, F. Mueller (lectotype *B. ciliaris* var. *subdissecta*, MEL); *Ritcairn, 8.9.1907, M. Mills (JMB); Berri, 1.1921, J. B. Cleland (JBC); Loxton, 12.2.1942, J. B. Cleland (JBC); Dublin, 25.8.1907, H.H.D.G. (JMB); Alawoona, 2.12.1913, J. B. Cleland (JBC); Alawoona, 5.10.1915, J. M. Black (JMB); Mannum "Cliff Pastures", 5.1924 (AD); Murray Bridge, 10.1911, H.H.D.G. (JMB); Murray R., 5.10.1848, F. Mueller (MEL); dry ridges on the Murray (MEL); Murray R., R. Tate (AD); Karoonda, 7.10.1915, J. M. Black (JMB); Karoonda, 16.8.1924, J. B.

- Cleland (JBC); Kinchina, 4.2.1937, J. B. Cleland (JBC); Tanunda Crk., 1.3.1848, F. Mueller (MEL); Port Vincent, 13.3.1907, J. M. Black (JMB); Holdfast Bay, 10.2.1848, 5.1851, F. Mueller (MEL); Holdfast Bay, "Sandhills", 27.10.1886 (AD); *Brighton, 18.9.1904, J. M. Black (JMB); Outer Harbour, 22.10.1932, J. B. Cleland (JBC); Hallett's Cove, 24.9.1932, J. B. Cleland (JBC); Mt. Lofty Ranges, 1847, F. Mueller (MEL); Change's Line, near Hartley, 12.10.1938, J. B. Cleland (JBC); Goolwa, 1.1940, J. B. Cleland (JBC); Port Victor, H.H.D.G. (JMB); Victor Harbour, 15.1.1913, J. M. Black (JMB); near Encounter Bay, "Sand near Sea", 7.1.1924, J. B. Cleland (JMB, JBC); Encounter Bay, "Scrub behind bluff", 2.1921, J. B. Cleland (JBC); between Bugle Range and L. Alexandrina, 27.4.1848, F. Mueller (MEL); *Tintinara, 12.40, E.C.B. (JMB); Coonalpyn, 5.1911, J. B. Cleland (JBC, NSW); Ooldea, 25.8.1922, 19.8.1939, J. B. Cleland (JBC); Ooldea, 9.1920, E. H. Ising (BRI); Wynbring, 20.8.1926, J. B. Cleland (JBC); Tarcoola, 19.9.1920 (JMB); Carooona, Iron Knob, W. L. Cleland (JBC); Whyalla, Knob, 1.9.1944, J. B. Cleland (JBC); *between Iron Knob and Franklin Harbour, 20.10.1912, J. Sircock (JMB); head of Great Australian Bight, 9.1879, R. Tate (AD); Nullabor Station, via Fowler's Bay, 8.1907, *10.1907, T. Brown (NSW); Fowler's Bay, A. Richards (AD); Cape Thevenard, 12.11.1915, J. M. Black (JMB); Minnipa, 12.1915, W. Stafford (AD); Tooligie, 10.11.1915, J. M. Black (JMB); Port Lincoln, Wilhelmi (MEL); Thistle Island, 1.1907, J. H. Maiden (NSW); "S.A.", 4.1849, Hildebrand (MEL).
- Western Australia*: 30 miles north of Meekatharra, 7.1938, W. E. Blackall (PERTH); Cue, 1931, A. B. Cashmore, n. 2010 (AD); Mt. Magnet, 9.1903, W. V. Fitzgerald (NSW); Laverton, 8.1931, Gardner and Blackall (PERTH); Skull Creek, Laverton, 8.1931, C. A. Gardner, n. 2449 (PERTH); Broadarrow, 10.1900, E. Kelso (PERTH); 100 miles north of Kalgoolie, 9.1905, C. Andrews (PERTH); Kalgoolie, 7.10.1914, C. H. Ostenfeld, n. 987 (PERTH); Muir Survey, Trans. Railway, 8.01, Anketell (PERTH); Coolgardie, 1896, A. J. Vagan (NSW), Fraser Range, 10.1891, R. Helms (MEL, AD); Champion Bay, 8.1899, A. Crawford (PERTH); Northam, 10.1900, J. H. Gregory (PERTH); Avon R., L. Preiss, n. 87; *Darling Range, Oldfield, "boggy places" (MEL); between Katanning and Pingrup, 9.1932, W. E. Blackall, n. 2991 (PERTH); Plantagenet and Stirling Range, Maxwell (MEL); between Ellen's Peak and Toll's Creek, 23.10.1902, A. Morrison (PERTH); West Beach, Esperance, 21.1.1944, H. M. Wilson, n. 80. (PERTH); behind Esperance, "sides of sandy track through bush", 30.1.1944, G. P. Whitley (NSW); Esperance Bay, "grassy sand flats" (MEL); Esperance 4.6.1945, G. P. Whitley (NSW); inland, Esperance Bay, and Cape Le Grande, "grassy flats" (MEL); interior, Cape Pasley, "sand plains" (MEL); "W.A.", C. A. Gardner, n. 2383 (PERTH).

Labillardière's specimens being unavailable for examination, the author is indebted to Professor H. Humbert, Director of the Natural History Museum, Paris, for a photograph of the herbarium sheet bearing these specimens and for the following information with regard to them: "Feuilles d'herbier de *Bellis ciliaris* comprenant 5 pieds sûr portant 6 capitules en mauvais état, sans fruits visibles." The photograph leaves no doubt as to the identity of the species, and a subsequent letter from Professor Humbert supplies further relevant details: "Les pédoncules et les bractées du *Bellis ciliaris* sont très finement pubescentes glanduleux; toutefois, cela ne se voit pas à l'oeil nu, mais seulement avec une très forte loupe." There is no evidence that Bentham examined Labillardière's specimens, apparently assuming their glabrous nature in the absence of any statement to the contrary in the original description. In the National Herbarium, Melbourne, there are three specimens from South Australia, and one from Western Australia, which were examined by Bentham prior to the publication of *Flora Australiensis*, and which are enclosed in a folder inscribed by Bentham, "var. *glandulosa*". One of these specimens, "W.A., J. Drummond, n. 210", was cited by him in the original description of the variety, and has accordingly been selected as lectotype of var. *glandulosa*. All these specimens are minutely glandular-pubescent distally, but none of them is any more so than various others, also examined by Bentham, but not included in this variety. The lectotype, in addition, is slightly woolly-hairy, and consequently has been transferred to var. *lanuginosa* (Steetz) Benth. Since it has been shown that Labillardière's specimens are also glandular-pubescent, the var. *glandulosa* is rejected.

Var. *sub-dissecta* Benth. is represented in the National Herbarium, Melbourne, by two specimens enclosed in a folder inscribed "var. *sub-dissecta*" by Bentham. Although stated to be glabrous in the original description, both of these specimens are finely glandular-pubescent distally. One of them, from Crystal Brook, has greatly enlarged leaves, suggesting a very moist and protected situation, and the segments are again divided as noted by Bentham. While this individual specimen is striking in appearance, it is held that the isolated exaggeration of a character which is not infrequently

indicated in the lower leaves of large specimens, does not merit varietal status. This specimen has been selected as lectotype of the variety, but the variety itself is not confirmed.

An authentic syntype specimen of var. *grandiflora* Benth. has not been available for examination, but the original description states: "Flower heads as large as in *B. iberidifolia*, but achenes of *B. ciliaris*." The size of the inflorescence in itself is a character of little or no significance in this genus, and unsupported by other more reliable criteria does not justify varietal rank.

B. Drummondii Walp. is taken as synonymous with *B. ciliaris* on Bentham's authority, as it has not been possible to trace any of Walper's specimens. His description agrees quite satisfactorily with this species.

The general appearance of specimens of this species is such that it can usually be determined on sight, though in certain specimens there is a strong resemblance to *B. iberidifolia*. Variation in the leaves is sometimes considerable, and though the leaf-segments are typically narrow-linear to linear, specimens have been seen from Broken Hill, western Victoria, and Mt. Lofty Ranges in which they are broad-linear. Lobing of the leaf may be confined to the distal end of the blade so that a petiole appears to be present, or the proximal lobes may be close to the stem, so that the leaf is sessile. This latter character is frequently exhibited by upper leaves in which the lobes often have the appearance of teeth, and it is interesting that specimens have been examined from Coonalpyn, Berri and Karoonda (south-eastern South Australia) in which the majority of the leaves exhibit this character. In large specimens the lobes of the lower leaves frequently bear some small teeth, and exaggeration of this condition is seen in the lectotype of var. *subdissecta*, from Crystal Brook, and has also been noted in a specimen from Western Australia (Gardner, 2383).

Though it is rare to find a glabrous plant, all degrees of glandular-pubescent are noted, from those in which the indumentum can only be detected microscopically, to others in which the plant is conspicuously glandular to the naked eye. Several specimens have been seen from localities around Broken Hill in which the glandular hairs are septate, and comparatively long.

The fruits of this species are remarkably constant, variation being limited to the wing of the disc florets, which may be entire, crenate or irregularly dissected, considerable variation frequently occurring within the same capitulum. In the State Herbarium, Perth, are two specimens, from Champion Bay (9.1899, A. Crawford) and "Between Ellen's Peak and Toll's Creek" (23.10.1902, A. Morrison), which agree with this species in all particulars except that there is no suggestion of a wing being present on the disc fruit, though these are slightly broader than those of the ray. In J. M. Black's herbarium is also a specimen from between Iron Knob and Franklin Harbour with the accompanying note, "all the fruit like the outer ones". Unfortunately no fruits remain on this specimen. These specimens may represent a subspecies of *B. ciliaris*, but until further specimens are collected they are retained within var. *ciliaris*.

Brachycome ciliaris (Labill.) Less. var. β *lanuginosa* (Steetz) Benth.

Fl. Aust., iii (1866), 519.

(Text-fig. 94; Plate vi, map 29.)

Synonymy: *B. lanuginosa* Steetz, Pl. Preiss, 1 (1845), 427.

Lectotype: "In Nova Hollandia (Swan River Colonia) in prom. horio Cape Riche, leg. cl. Dr. Preiss (Herb. Preiss No. 85), emi 1843" (MEL).

Lectoparatype: l.c. (MEL).

Stems more or less white woolly, with usually short glandular hairs present distally. Leaves cauline, up to 3.4 cm. long, pinnatisect, the lobes 3-9, up to 1.3 cm. long, 1.5 mm. broad, narrow linear to linear, pungent pointed.

Habitat: Rather dry sandy situations.

Range: Throughout Australia south of the Tropic of Capricorn.

Specimens examined:

Queensland: Ten miles N.W. of Longreach, "Sand-ridge", 28.5.1936, S. L. Everist and C. T. White, n. 113 (BRI); Barcarolle, Longreach, 23.9.1934, F. L. Berney, n. 123 (BRI); near Nochnagar "in *Eucalypt* forest on fine sand, about 1,100 ft. Bushy dull-green annual

about 6 ins.", 29.11.1935, S. T. Blake (BRI); Jericho, 4.1946, M. S. Clemens (BRI); Northampton Downs near Blackall, "Sandy land on Dead Finish Country", 26.8.1935, S. L. Everist, n. 1293 (BRI); Mitchell district, Blackall, "tufted erect herb on sandy aerodrome", 24.8.1935, S. L. Everist, n. 1226 (BRI); Warrego district, Carbean, common on sand ridges. Perennial herb, flowers mauve", 26.3.1941, C. T. White, n. 11824 (BRI); Warrego River, 9.1885 (BRI).

New South Wales: Tibooburra, 5.1930, O. Couch (NSW); Bulloo Overflow, "Sandhills", spring, 1941, N. C. W. Beadle (NSW); Co. Yantara, "Creek", spring, 1941, N. C. W. Beadle (NSW); Co. Ularara, "Mulga scrub", 8.1941, N. C. W. Beadle (NSW); near Carinda, "Under trees of Wilga. Brown clay loam", 9.1942, N. C. W. Beadle (NSW); Balmoral Station, Gunnedah, 9.1910, J. W. Hodgson (NSW); Coolabah, 6.1901, J. L. Boorman (NSW); Cobar, "Scrub, red loam", N. C. W. Beadle (NSW); 50 miles S.W. of Cobar, "Under trees of *Callitris glauca* and *Geijera*", 6.1944, N. C. W. Beadle (NSW); Shuttleton, 10.1903, W. Bauerlein (NSW); Narromine, 4.1913, E. Breakwell (NSW); near Mt. Danbury, 48 miles N.W. of Wilcannia, "Gibber plains, in slight depressions in small 'creeks'", 8.1944, N. C. W. Beadle (NSW); Wilcannia district, 26.8.1939, J. Vickery and I. Pidgeon (NSW); Tandarlo via Wilcannia, 1886, B. Kennedy (MEL); Fowler's Gap, 75 miles N. of Broken Hill, "in a sandy creek", 8.1944, N. C. W. Beadle (NSW); Stephen's Creek, Broken Hill, 12.8.1928, A. Morris (BRI); Broken Hill, 28.11.1919, 1.1920, 2.9.1920, A. Morris (NSW); Broken Hill, 12.1917, E. C. Andrews (NSW); Broken Hill, 16.10.1943, C. E. Chadwick (NSW); Rocky Range, Umberumberka, 9.1946, N. C. W. Beadle (NSW); Menindee, Sandhills, 9.1946, N. C. W. Beadle (NSW); 10 miles E. of Pooncarie, "red brown sandy soil", 8.1942, N. C. W. Beadle (NSW); near Wentworth, "Mallee, red sandy soil", 6.1942, N. C. W. Beadle (NSW); between Euston and Mildura, 19.8.1946, J. Vickery (NSW); Darling Desert, Dallachy (MEL); Darling R., "Sandhills", Victorian Exped. (MEL).

Victoria: Murray R., J. Dallachy (MEL); Nathalia, 10.1930, J. H. Willis (MEL).

Central Australia: Osborne Ranges, rocky hill, quartzite, 7.1922, C. E. F. Allen (NSW); MacDonnell Ranges, "herb up to 2 ft. high", 7.1922, C. E. F. Allen (NSW); Arltunga goldfields, 7.1922, C. E. F. Allen (NSW, BRI); *north of Alice Springs, 1882, E. Flint (MEL); near Stanley Chasm, about 30 miles W. of Alice Springs, 15.12.1942, A. Ward (BRI); Alice Springs, 1895, O. E. Menzel (NSW); Crown Point, Finke River, 19.5.1913, S. A. White (JMB); Finke R., 17.5.1894, R. Tate (AD).

South Australia: 30-80 miles E. of Ernabella, 23.9.1945, J. B. Cleland, (JBC); Ernabella, 17.7.1943, L. B. Young (MEL); Ernabella, Giblin's Well, "open country", 13.7.1943, L. B. Young (RAB); Musgrave Ranges, 7.1926, H. Basedow (JMB); south of Charlotte Waters, Canterbury Crk., 1885, F. Mueller (MEL); Warrina, 5.1891, R. Helms (AD); Lake Eyre, Schomburgk (AD); Anna Creek, 26.8.1931, J. B. Cleland (JBC); Hergott to Strangeways, W. L. Cleland (JBC); *Beresford, 4.8.23, J. B. Cleland (JMB); Beresford, 10.9.1930, 26.8.1931, J. B. Cleland (JBC); Beresford, 25.8.1932, *4.8.1933, J. B. Cleland (JBC); Beresford, 8.1942, L. Fuauz (MEL); Coward Springs, 10.9.1930, J. B. Cleland (JBC); Wangianna, 4.9.1941, J. B. Cleland (JBC); Hergott Springs, 1896, O. E. Menzel (AD); Mt. Lyndhurst Knob, J. M. Black (JMB); Mt. Lyndhurst, 8.1898, M. Koch (AD, NSW, BRI); Flinder's Range, 9.1898, M. Koch (JMB); Wilpena Pound, 10.11.1928, J. B. Cleland (JBC); Whittida, W. of Lake Torrens, 31.3.1930, B. J. Murray (AD); Gibbers Arcoona, W. of Lake Torrens, B. J. Murray (AD); Barton, 23.4.1931, C. E. Hubbard, n. 8335 (BRI); Kingoonya, 9.1920, E. H. Ising (NSW, MEL); Yudnapinna, 6.3.1945; N. T. Burbidge (AD); Hawker, plain, J. M. Black (JMB); Koonamore, 19.8.1931, 8.1939, C. M. Eardley (AD); Dublin, 8.9.1907, J. M. Black (JMB); *Brighton, 9.1904, J. M. Black (NSW); Mantung, 18.2.1924, J. B. Cleland (JMB, JBC); Renmark, 1.1936, C. M. Eardley (AD); Renmark, 3.10.1915, 30.10.1915, J. M. Black (JMB); Berri, 6.1942; C.D.B. (JMB); Berri, 2.10.1915, J. M. Black (JMB); Loxton, 21.8.1924, J. B. Cleland (JBC); Blanchetown, 8.1881, R. Tate (AD); Murray Bridge, 1.1907, J. H. Maiden (NSW); *Karoonda, 16.8.1924, J. B. Cleland (JBC); Kinchina, 10.10.1925, J. B. Cleland (JBC).

Western Australia: Murchison R., Oldfield (MEL); Cue, 1931, A. B. Cashmore (AD); Laverton, Skull Crk., 8.1931, C. A. Gardner, n. 2449 (PERTH); between Leonora and Malcolm, 11.9.1939, W. E. Blackall, n. 4127 (PERTH); Coolgardie, 7.1899, R. Helms (PERTH, NSW); Lakeside, 8.1898, W. V. Fitzgerald (NSW); between Katanning and Pingrup, 9.1932, W. E. Blackall, n. 2991 (PERTH); Plantagenet and Stirling Ranges, Maxwell (MEL); *valley between Stirling Ra. and Phillip's R., 10.1903, C. Andrews (PERTH); Cape Riche, L. Preiss, n. 85 (lectotype and lectoparatype of *B. lanuginosa*, also of *B. ciliaris* var. *lanuginosa* MEL); Jacup R., 1903, C. R. P. Andrews (NSW); Phillip's R., n. 233 (MEL); *Esperance Bay, 1881, Dempster (MEL); Esperance, West Beach, 21.1.1944, H. M. Wilson, n. 80 (PERTH); behind Esperance, "side of sandy tracks through bush", 30.1.1944, G. P. Whitley (NSW); Esperance, 7.2.1944, G. P. Whitley (NSW); *Israelite Bay, 12.1884, Brooke (MEL); Eucla, 1886, W. D. Batt (MEL); "W.A.", J. Drummond, n. 86, n. 211, n. 387 (MEL); "W.A.", J. Drummond, n. 210 (lectotype of *B. ciliaris* var. *glandulosa*, MEL).

The specimens selected as lectotypes and lectoparatypes are mounted on a herbarium sheet labelled "*B. lanuginosa nobis*" and otherwise annotated in Steetz's handwriting. Both these specimens were subsequently examined by Bentham and quoted in his original description of var. *lanuginosa*, as well as various other specimens now in the National Herbarium, Melbourne (Darling Desert, Dallachy; Western Australia, Drummond, n. 86, and 211).

This variety occupies the same extensive range as var. *ciliaris* and remarkably little correlation has been found between the amount of indumentum present and the geographical position of the specimens. Throughout the range there is considerable variation in the amount of woolly hairs borne by specimens even from the same locality, varying from a dense white indumentum in some specimens, to others in which a careful search is necessary to detect a cluster of such hairs only at the junction of leaves and stem. In general, dense woolliness of the stems is a feature of specimens from western New South Wales, northern South Australia and Central Australia, but all specimens from these regions are not necessarily woolly to this extent.

B. ciliaris (Labill.) Less. var. γ *lyrifolia* (J. M. Black), comb. nov.

(Text-fig. 95; Plate vi, map 29.)

Synonymy: *B. lyrifolia* J. M. Black, *Trans. Roy. Soc. S.A.*, lxi (1937), 249.

Lectotype: Chamber's Creek, Flinder's Range, 6.37, E. C. Black (MEL).

Lectoparatypes: Three, l.c. (JMB).

Ascending herbs, shortly glandular all over. Leaves rather flaccid lyrate to obovate, 1-4 cm. long, including the petiole, about 1 cm. broad. Lobes or teeth 2 to usually about 7, irregularly placed.

Range: Apparently confined to Flinder's Range, South Australia.

Specimens examined: *Mt. Lyndhurst, 8.1898, M. Koch, n. 346 (BRI); Mt. Chambers, Flinder's Range, 29.5.1937, J. B. Cleland (JBC); Chamber's Creek, 6.1937, E. C. Black (lectotype, MEL; lectoparatypes, JMB).

As a large proportion of the capitula do not set seed, mature fruit are sometimes difficult to find, and for this reason their dimorphic nature has not been previously recorded. These fruits, however, are identical with those of *B. ciliaris*, and for this reason specific status must be withdrawn.

This variety, in habit and characters of the leaves, is quite distinct from any other and is apparently very localized in its distribution. Among the localities mentioned in the original description is "Mt. Gillen, Central Australia, Aug., 1936, E. C. Black". This specimen, in J. M. Black's personal herbarium, consists only of three leaves and an inflorescence with extremely young fruits. It is not listed in the distribution of the variety in the present work as the author is not satisfied with the identification.

B. ciliaris (Labill.) Less., var. δ *subintegrifolia* var. nov.

(Text-fig. 96; Plate vi, map 29.)

Holotype: Tamworth, 4.42, Consett Davis (NSW).

Paratypes: Five, l.c. (MEL, BRI, AD, PERTH, HO).

Folia ad 3.2 cm. longa, 1 mm. lata, angusta-linearia-linearia, acute-acerba, integra aut in basi 1-3 lobis filiformibus.

Leaves up to 3.2 cm. long, 1 mm. broad, narrow-linear to linear, pungent-pointed, all entire or some with 1-3 filiform segments proximally.

Habitat: Grassland and scrub.

Range: Darling Downs district of Queensland, Tamworth in New South Wales, northern to western Victoria and south-eastern South Australia.

Specimens examined:

Queensland: Wandoan, "in low forest (Brigalow and Belah scrub) up to 10 ft. high, grey soil", 890 ft., 15.11.1930, C. E. Hubbard (BRI); Bybera, 20.9.1944, C. T. White, n. 12619 (BRI).

New South Wales: Four miles north of Tamworth, 6.1.1942, Consett Davis (NSW, MEL). Tamworth, 4.1942, Consett Davis (holotype, NSW, paratypes, MEL, NSW, BRI, AD, PERTH); Gulgong, 4.1901, J. H. Maiden and J. L. Boorman (NSW).

Victoria: Echuca, 1884, H. King (MEL); Rutherglen, 12.1910, H. B. Williamson (MEL); Co. Borung, 10.5.1903, F. M. Reader (MEL); Lowan, 11.11.1898, F. M. Reader (MEL); Lake Victoria, 28.4.1878, F. Mueller (MEL).

South Australia: *Lake Alexandrina, 4.1848, F. Mueller (MEL); "S.A.", O. Tepper (MEL).

The leaves of the above series show a certain amount of variation apart from size. In some specimens all those present have entire margins, but in others a certain number of them bear one or more filiform segments confined to the proximal half of the blade. These segments come off almost at right angles to the leaf, and are quite irregularly arranged, so that it is not unusual to find two segments on one side of the leaf and none on the other. In no case does the method of division approximate to that shown in var. *ciliaris*, in which the segments are usually distal in position and subtend an angle of about 45° with the midrib.

The distribution of this variety as at present recorded is somewhat discontinuous, but further collecting will probably produce specimens in the northern and southern tablelands of N.S.W. The fact that none have been collected from coastal areas indicates that it is essentially an inland variety.

As regards affinities within the species, var. *subintegrifolia* is most closely allied to var. *lanuginosa* in its constant possession of a small amount of white woolly hairs, particularly in the leaf-axils. Some short glandular hairs may also be present, but not invariably so.

Plants raised from fruit from the paratypes are identical with the parent plant, indicating that it is a true breeding variety. These plants are now four years old, and are still in vigorous growth.

9. Superspecies CILIOCARPA.

47. BRACHYCOME CILIOCARPA W. V. Fitzgerald.

(Text-figs. 107, 114, 115; Plate vi, map 30.)

Jour. W.A. Nat. Hist. Soc., ii (1905), 23.

Lectotype: Cue, 1.1903, C. P. Andrews (PERTH).

Lectoparatype: I.c. (NSW).

Glabrous annuals with many branching stems arising from the base, from 12.5 to 32 cm. high, with radical and cauline leaves, the inside of the leaf bases being sparsely septate hairy. Leaves pinnatisect, up to 6.5 cm. long, the lobes up to 2.2 cm. long, 1.1 mm. broad, narrow-linear to linear, obtuse, entire or occasionally lobed. *Peduncles* robust, terminal or axillary, leafy proximally. *Capitula* up to about 65, 8–12 mm. diameter across the bracts. *Involucral bracts* about 14, 4.5–6.5 mm. long, 1.5–3.5 mm. broad, ovate, subacute, entire or slightly serrulate, glabrous. *Ray florets* 12–15, the rays violet, 1.2–1.5 cm. long, 2.4–5 mm. broad. *Receptacle* slightly pitted, up to 2.2 mm. broad, 2.4 mm. high, steeply conical. *Fruit* light brown, about 2.4 mm. long, 1.1 mm. broad, cuneate, flattened, four-angled, apically rounded, the centre of each face slightly depressed and bearing many long curled hairs; fruit laterally smooth and glabrous except for a median longitudinal ridge bearing many long curled hairs, the uppermost of which, together with those of the face, are intermingled with the conspicuous pappus bristles.

Habitat: Under cover of scrub.

Range: South-western Queensland to north-western New South Wales, and mainly interior of Western Australia.

Specimens examined:

Queensland: Pitherty, south of Eulo, "red sandy surfaced soil with Buddah, Ironwood and Mulga. Small annual, not common, growing under cover of *Bassia Birchii*", 19.9.1944, G. H. Allen (CSIR); Yanco, S.W. Q'land, "lavender", 8.9.1923, W. MacGillivray (BRI).

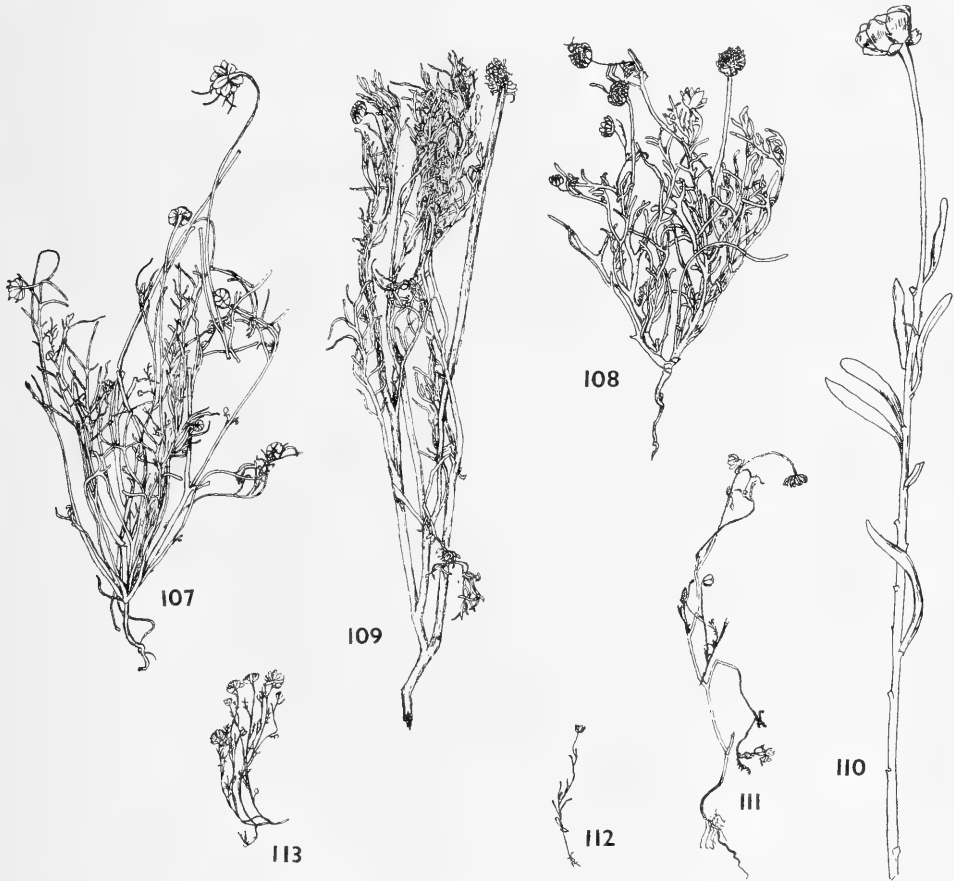
New South Wales: Paroo district, 9.1900, E. Betche (NSW); Waverley Downs to Hungerford, 10.1912, J. L. Boorman (NSW); *Co. Thoulcanna, Mulga Scrub, Spring, 1941, N. C. W. Beadle (NSW); *Warroo, via Bourke, 10.1938, K. I. Morris (NSW); Tibboburra, "annual, lavender ray, yellow centre. Among scrub", 10.1920, W. MacGillivray (NSW).

Western Australia: Shark Bay, 10.77, F. Mueller (MEL); Upper Murchison R., near Mt. Hale, 1884, C. Crossland and F. Mueller (MEL); Meekatharra, "annual, 4 ins. Ray florets violet. Red loamy stony soil", 16.7.1931, C. A. Gardner, n. 2305 (PERTH); Cue, 1.1903, C. Andrews (lectotype, PERTH; lectoparatype, NSW); Leonora, "flowers mauve", 9.1939, W. E. Blackall (PERTH); *Watheroo Rabbit Fence, 9.1905, M. Koch (PERTH).

The fruits are not dimorphic as indicated by Fitzgerald, but examination of syntype and other material reveals that the inner disc fruits are usually immature and possibly never reach maturity. The fruits increase in thickness with age, and in the Murchison

R. specimen those on the outside are actually square. At maturity the longest of the silky hairs disappear; the remainder are closely appressed to the fruit and the uppermost of these intermingle with the bases of the pappus bristles. The specimen from Eulo differs vegetatively from the Western Australian specimens in that it is glandular, particularly distally, and septate hairs were not found. The fruits agree with those of the Murchison *R. specimen*, which suggests that the fruits of the lectotype are not quite mature.

The specimens from Sharks Bay show the only vegetative variation noted, in that while one or two leaves are pinnatisect, the majority are linear and entire.



Text-figures 107-113. Habit studies. $\times \frac{1}{2}$.

107, *B. ciliocarpa* (Lectotype). 108, *B. oncocarpa* (Lectotype). 109, *B. cheilocarpa* (Lectotype). 110, *B. latisquamea* (Lectotype). 111, *B. glandulosa* (Lectotype). 112, *B. perpusilla* var. *perpusilla* (Lectotype). 113, *B. perpusilla* var. *tenella*.

48. BRACHYCOME ONCOCARPA Diels. Engl. Jahrb., xxxv (1904), 606.

(Text-figs. 108, 116-118; Plate vi, map 30.)

Lectotype: Carnarvon, W.A., viii, 1901, L. Diels, n. 4286 (MEL, ex Herb. Königl. Botanischer Garten und Museum).

Erect leafy annuals branching from the base, 10.5-15 cm. high, glabrous or very sparsely woolly proximally, and at leaf-stem junctions. Leaves radical and cauline. Radical leaves up to 5 cm. long, pinnatisect, the lobes up to 8 mm. long, 1.1 mm. broad. Cauline leaves up to 6 cm. long, pinnatisect, the lobes 1-6, irregularly spaced, linear, obtuse, 4-8 mm. long, 1 mm. broad. *Peduncles* terminal or axillary, up to 11.5 cm. long, naked or with a single, entire, narrow-linear leaf at the centre. *Capitula* up to 24,

terminal, 5–10 mm. diameter. *Involucral bracts* about 14, 3.5 mm. long, 1.8 mm. broad, entire or minutely serrulate, obovate, obtuse to sub-acute, with a few minute glandular hairs on the outer surface. *Receptacle* convex, 1 mm. high, 1 mm. broad. *Ray florets* "mauve". *Fruit* light-brown, 2–2.5 mm. long, 1–1.2 mm. broad at the summit, laterally compressed, shouldered distally, the inner face bearing three longitudinal ridges lateral to which are longitudinal areas of long glandular hairs; glandular hairs also present at the base of the fruit, the summit of the smooth outer margin, and on the compressed area of each side. Pappus conspicuous, stellate.

Range: Western Australia.

Specimens examined: Carnarvon, 8.1901, L. Diels, n. 4286 (lectotype, MEL, ex herb. Königl. Botanischer Garten und Museum); near Pindar, 9.1931, W. E. Blackall (PERTH).

This rare species is known from only two specimens, only one of these, the lectotype, bearing fully mature fruit. In vegetative features it is very similar to *B. ciliocarpa*, the main differences being the smaller number of leaf segments. The fruit structure is elaborate, and although basically similar to that of *B. ciliocarpa*, is quite distinctive and unlike any other species.

49. BRACHYCOME CHEILOCARPA F. Muell., *Southern Science Record*, ii (1882), 172.

(Text-figs. 109, 119; Plate vi, map 31.)

Lectotype: Gascoyne River, W.A., J. Forrest (MEL).

Lectoparatype: l.c. (MEL).

Branching erect or ascending plants, probably perennial, 18–35 cm. high, bearing long septate hairs on stems and leaves. Leaves cauline, up to 6 cm. long, pinnatisect; segments 10–13, linear, obtuse, up to 1.3 cm. long, 0.5–1.2 mm. broad, usually entire but sometimes lobed, irregularly arranged or alternate. *Peduncles* axillary and usually robust, up to 13 cm. long, 2 mm. diameter, slightly thicker distally, glabrous and naked except for a single proximal leaf. *Capitula* up to 13, 0.8–1 cm. diameter. *Involucral bracts* about 12, 5.5–6 mm. long, 1.2 mm. broad at the base, lanceolate, entire, the apex filiform, the outer surface bearing a few long septate hairs. *Ray florets* about 14, 8 mm. long, 1.2 mm. broad, "pale violet". *Receptacle* broadly and steeply conical, about 3 mm. high, 2 mm. broad. *Fruit* straw-coloured, 2.6 mm. long, 1.5 mm. broad distally, cuneate, the body flattened, bearing a few glandular hairs or tubercles in a central depression, apically distended into a bladder-like swelling on each face; wing narrow and undulating, the margins bearing long glandular hairs. Pappus conspicuous, consisting of bristles of irregular length, stellately arranged.

Range: North-western Western Australia.

Specimens examined: Gascoyne River, J. Forrest (lectotype and lectoparatype, MEL); Gascoyne River, 60 miles east of Carnarvon, 20.9.1941, C. A. Gardner, n. 6061, "erect or ascending, 6–10 ins. high. Ray florets pale violet. Red sand" (PERTH); *9 miles north of Meekatharra, "Sandy red loam", 17.7.1931, C. A. Gardner (PERTH).

This species is most closely related to *B. ciliocarpa* Fitz., the mode of growth and general vegetative appearance of the two species being very similar, but characters of the fruit and involucral bracts make them readily distinguishable.

The fruit can be regarded as basically of the *B. ciliocarpa* type, with the addition of "shoulders" not unlike those occurring in *B. oncocarpa*, and in addition, a narrow wing which is not seen in the other species of this group.

10. Superspecies LATISQUAMEA.

50. BRACHYCOME LATISQUAMEA F. Muell., *Fragm.* xi (1878), 16.

(Text-figs. 110, 120; Plate vi, map 31.)

Lectotype: Shark Bay, ? 1877, F. Mueller (MEL).

Lectoparatypes: Eight, l.c. (MEL).

Erect perennials up to 2 m. high, glabrous, with woody stems and thick tap root. Leaves cauline, entire, sessile, narrow-lanceolate to lanceolate, obtuse to entire, up to 5.7 cm. long, 8 mm. broad, with often a small shoot or cluster of linear leaves in the axils. *Peduncles* terminal or axillary, leafy. *Capitula* numerous, 1.5–2 cm. across the involucral bracts. *Involucral bracts* imbricate, 12–16, obtuse to bluntly acute, glabrous,

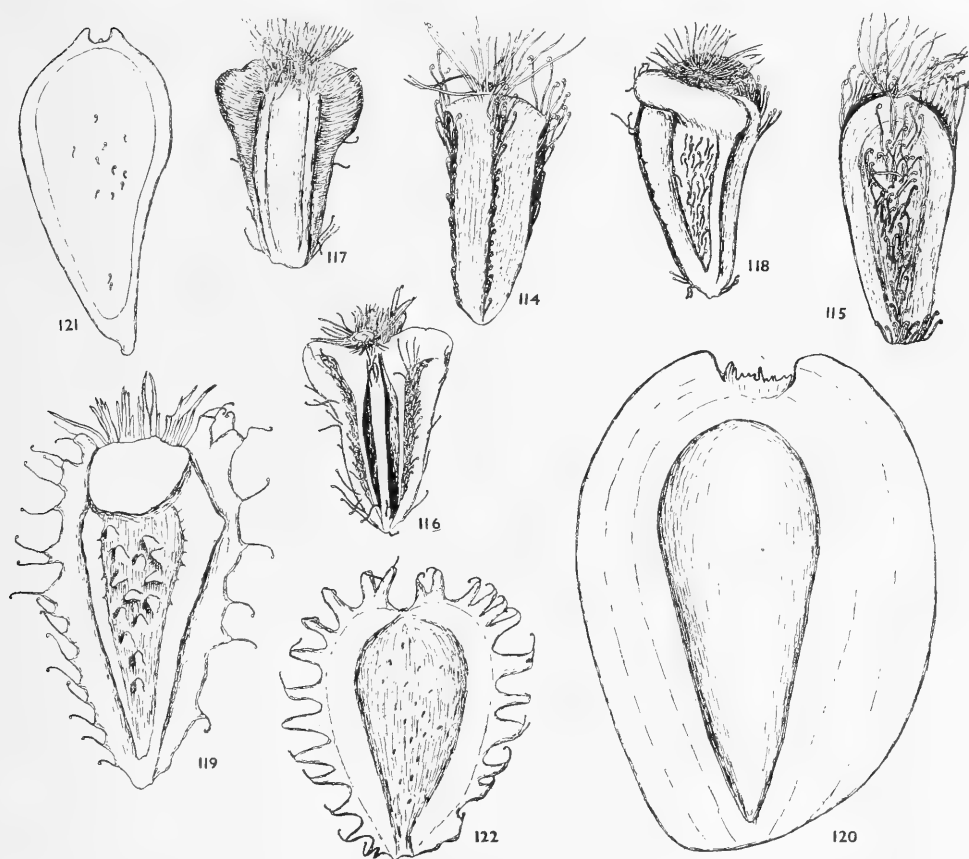
entire or irregularly toothed; outer bracts 5-6 mm. long, 4-7 mm. broad, obovate; inner bracts usually linear-cuneiform. Rays 30-50, 1.5-2.3 cm. long, 2-2.5 mm. broad, "white", "pale violet", "lilac". Receptacle convex, 3.5-5 mm. broad, 1.5 mm. high, shallowly pitted. Fruit 3.2-3.5 mm. long, 1.8-2.5 mm. broad, light brown, broadly obovate, the central body not well defined, surrounded by a broad, entire wing. Some outer fruits occasionally developing an extra wing, giving them a triangular appearance. Pappus a ring of minute irregular teeth.

Habitat: Sandy soil near coast.

Range: North-west coast of Western Australia.

Specimens examined:

Western Australia: Point Coates. "Sand dunes behind beach", 4.10.1944, G. P. Whitley (NSW, BRI); Carnarvon, "Sand dunes", 14.8.1932, C. A. Gardner, n. 3019 (PERTH); Carnarvon, 12.1906, W. V. Fitzgerald (NSW); Unilyala R., 1882, J. Forrest (MEL); Shark Bay, ? 1877, F. Mueller (lectotype and lectoparatypes, MEL); Hamelin Pool, "red sand, 6 ft., semiscandent. Ray flowers pale violet", 25.8.1931, C. A. Gardner, n. 2544 (PERTH).



Text-figures 114-122. Fruit. $\times 17$ approx.

- 114, *B. ciliocarpa*. Outer surface of fruit. 115, *B. ciliocarpa*. Lateral surface of fruit.
 116, *B. oncocarpa*. Inner surface of fruit. 117, *B. oncocarpa*. Outer surface of fruit.
 118, *B. oncocarpa*. Lateral surface of fruit. 119, *B. cheilocarpa*. 120, *B. lat squamea*.
 121, *B. glandulosa*. 122, *B. perpusilla*.

This species can be readily identified at any stage by its large and woody habit, size of inflorescence and fruit. There appears to be no intra-specific variation, but owing to the restricted range of this species it has not been possible to examine a large

series. On account of the large size of individual plants, herbarium specimens consist only of branches, so that it has not been possible to estimate the average number of inflorescences borne by plants.

11. Superspecies SILPHIOSPERMA.

51. BRACHYCOME GLANDULOSA (Steetz in Lehmann) Benth.

Fl. Aust., iii (1866), 521.

(Text-figs. 111, 121; Plate vi, map 32.)

Synonymy: *Silphiosperma glandulosum* Steetz in Lehmann Pl. Preiss. i (1845), 433.

Lectotype: "New Holland, Swan River Colony, L. Preiss, n. 103, received 1843" (MEL).

Lectoparatypes: Three, l.c., MEL.

Slender erect branching annuals up to 21 cm. high, densely glandular-hairy all over, particularly distally. Leaves cauline, sessile, up to 3.9 cm. long, pinnatisect, the segments up to 1.5 cm. long, 1 mm. broad, narrow to broad-linear, shortly mucronate. First pair of cauline leaves when present up to 6.5 mm. long, 1.5 mm. broad, spatulate, entire, obtuse, connate. *Peduncles* slender, leafy proximally. *Inflorescences* up to 16, 6-7 mm. diameter. *Involucral bracts* 12-15, 2.5-4 mm. long, 1.5-2.7 mm. broad, elliptical, sub-acute, densely glandular, with slightly torn-ciliate margins. *Ray florets* 8-10, the rays white, 1.1 mm. long, 0.3 mm. broad, hardly exceeding the bracts. *Receptacle* 0.7-1 mm. high, 1.5-1.8 mm. broad, slightly convex, not pitted. *Fruit* up to 3 mm. long, 1.8 mm. broad, obovate, flat; the body straw-coloured and slightly curved, the concave surface facing the centre of the receptacle; margin broad, smooth and entire, golden-brown, excised at the apex. Pappus absent.

Distribution: Apparently confined to inland districts of Western Australia.

Specimens examined: Boulder, 8.1898, W. V. Fitzgerald (NSW); Midland Junction. "rays white", 9.1900, W. V. Fitzgerald (PERTH); Swan River Colony, L. Preiss, n. 103 (lectotype and lectoparatypes, MEL, PERTH).

From the small number of specimens in Australian herbaria it would seem that this species is a rare one. On the other hand, the inconspicuous nature of the flowers makes it possible that it has been overlooked by collectors.

The four syntype specimens are all mounted on the same herbarium sheet bearing identification (*Silphiosperma glandulosum nobis*) and locality data in Steetz handwriting. The pencilled "B" also occurs on the sheet, indicating that these specimens were examined by Bentham. Since they are quoted by Bentham in his description of *B. glandulosa* (1866) the type selection made covers both *Silphiosperma glandulosum* and *Brachycome glandulosa*.

52. BRACHYCOME PERPUSILLA (Steetz in Lehmann) J. M. Black.

Fl. South Aust., Pt. 4 (1929), 587.

Erect or weakly erect annuals, 1.2-10.5 cm. high, unbranched or branched, glabrous to sparsely glandular-pilose. Leaves cauline, up to 2.6 cm. long, entire or pinnatisect, the lobes up to 1 cm. long, narrow- to broad-linear, mucronate, reduced to hairs along the sheathing bases of the lower leaves. In young or small plants the lowest cauline leaves are connate and narrow obovate, the pair above is doubtfully connate and linear, while the remaining leaves are alternate. *Peduncles* filiform, often leafy. *Capitula* 1-20, 3-6 mm. diameter. *Involucral bracts* 5-9, 2-3 mm. long, 1-1.5 mm. broad, obovate, glabrous or sparsely glandular-pilose, acute, entire. *Ray florets* up to 18, rays about 1 mm. long, 0.5 mm. broad, white. *Receptacle* about 0.5 mm. broad, 0.3 mm. high, slightly convex, not pitted. *Fruit* 2-2.2 mm. long, 1-1.5 mm. broad, obovate, flat brown, the body bearing a few short glandular hairs, and surrounded by a wide thick wing-like margin which is deeply dissected into narrow, acute lobes each terminating in a long glandular hair. Pappus absent.

Key to the varieties.

- (1). Plant erect, glabrous, with an unbranched filiform stem. Leaves linear and entire, rarely with three minute teeth var. *a perpusilla*
 (1).* Plant weakly erect with several branching stems, sparsely and microscopically glandular-pilose. Leaves pinnatisect var. *β tenella*

Brachycome perpusilla (Steetz) Benth., var. *a perpusilla* comb. et stat. nov.

(Text-figs. 112, 122; Plate vi, map 32.)

Synonymy: *Silphiosperma perpusillum* Steetz in Lehmann, Pl. Preiss, i (1845), 434. *Brachycome collina* (Steetz in Lehmann) Benth., var. *perpusillum* (Steetz in Lehmann) Benth., Fl. Aust., iii (1866), 520.

Lectotype: New Holland (Swan River Colony), L. Preiss, No. 2416 (MEL).

Lectoparatypes: Ten, l.c. (MEL).

Very slender glabrous plants up to 5.5 cm. high, sparsely leafy, the lowest leaves always connate, obovate, about 3 mm. long, 1 mm. broad. Remainder of leaves linear, entire or with 3 minute teeth, acute, about 6 mm. long, 1 mm. broad with sheathing bases. *Capitula* one to each plant 3 mm. diameter. *Involucral bracts* 5-7, 1.8 mm. long, 0.3 mm. broad, glabrous, sub-acute, narrow-elliptical.

Range: Nonning to south-east of South Australia. Swan R. district in Western Australia.

Specimens examined:

South Australia: Nonning, 25.8.1928, J. B. Cleland (JBC); Highbury, 4.9.1880, R. Tate (AD); Kinchinda, 17.9.1927, J. B. Cleland (JBC).

Western Australia: Swan River Colony, L. Preiss, n. 2416 (lectotype, lectoparatypes, MEL).

The syntype specimens, from which lectotype and paratypes were selected, are enclosed in an envelope attached to a herbarium sheet annotated by Steetz. The note accompanying the locality data, "emi. 1843" is taken to be the date these specimens were received by Steetz, and predates the publication of his description of *Silphiosperma perpusillum* by two years.

The paucity of specimens of this variety in herbaria is probably due more to the insignificant nature of the plants than to their rarity in nature. In two instances (Kinchinda and Nonning) specimens were found mixed with dwarf plants and *B. lineariloba*, and in each instance the vegetative similarity between the specimens was remarkable.

Although no data are available with regard to habitat, it is probable that these plants occupy an environment involving a short growing period, in which germination, growth and reproduction must take place within a few weeks. Vegetative growth would then be reduced to a minimum, and fruit produced in the shortest possible time before desiccation occurred.

Brachycome perpusilla (Steetz) Benth., var. *β tenella* (Turez.) comb. nov.

(Text-fig. 113; Plate vi, map 32.)

Synonymy: *Brachycome tenella* Turez. *Bull. Soc. Imp. Nat. Mosc.*, xxiv (1851), 175. *Silphiosperma collinum* Sond., *Linnaea*, xxv (1852), 483. *Brachycome collina* (Sond.) Benth., Fl. Aust., iii (1866), 520.

Glandular plants, usually relatively robust and leafy. Leaves sessile with a sheathing base, the lowest pair connate, entire and spatulate, only found on small specimens; remainder pinnatisect, up to 2.6 cm. long, with linear, mucronate lobes, up to 6 mm. long, 0.9 mm. broad; uppermost leaves smallest, usually entire or minutely toothed. *Peduncles* more or less leafy. *Capitula* 1-7, 5-6 mm. diameter. *Involucral bracts* 3-3.5 mm. long, 1.5-2.1 mm. broad, keeled.

Range: Central and western Victoria to south-eastern South Australia, inland districts of Western Australia.

Specimens examined:

Victoria: Wimmera, Dallachy (MEL, NSW); S. Wycheproof, 9.1918, W. W. Watts (NSW); Axe Creek, F. Mueller (NSW); Puckapunyal, "rays white", 9.1942, Consett Davis (BRI, HO, NSW); Northwood, 9.8.1942, Consett Davis (NSW, MEL); Talarook, 12.10.1942, Consett Davis (NSW, MEL); foot of Mt. Alexander, F. Mueller (MEL); Skipton, W. Whan (MEL); Mt. Emu Creek, 11.1853, F. Mueller (MEL); Hopkin's R., 11.1853, F. Mueller (MEL); Grampians, 11.1901, H. B. Williamson (NSW).

South Australia: Nonning, 25.8.1928, J. B. Cleland (JBC, JMB); Wirrabara, 21.9.1906, J. M. Black (JMB); Port Lincoln, 10.1883, S. Dixon (AD); Adelaide, F. Mueller (lectotype and three lectoparatypes of *Silphiosperma collinum*, MEL); Holdfast Bay, 2.1851, F. Mueller (MEL); National Park, 6.10.1940, J. B. Cleland (JBC); Devil's Gully, R. Tate (AD); Kinchinda, 9.10.1926, 17.9.1927, J. B. Cleland (JBC, JMB); Encounter Bay, 30.8.1924, J. B. Cleland (JBC, JMB).

Western Australia: Cue, 7.1903, C. Andrews (PERTH); Boulder, 8.1898, W. V. Fitzgerald (PERTH, NSW); Lakeside, 8.1898, W. V. Fitzgerald (NSW).

The only syntype specimens which have been traced of *Brachycome tenella* ("New Holland, Drummond, Coll. iv, n. 208") are at Kew, and for this reason selection of a lectotype has not been possible. Bentham lists this species in the synonymy of his *B. collina* var. *perpusilla*, but this procedure is, in the present author's opinion, incorrect. Turczaninow, in his original description of *B. tenella*, states: "One stem, 1-3 branchlets each with one head; outer radical leaves and uppermost cauline leaves linear, elongate and entire, remaining leaves pinnatifid, toothed, more or less stem-clasping at base". These details, together with the ensuing description of the fruit, make it quite clear that the specimen described by Turczaninow is identical with Sonder's *S. collinum*, but not with *S. perpusillum* Steetz. Lectotype and lectoparatypes of *S. collinum* have been nominated, but the name itself reduced to synonymy. Black (1929) correctly abandoned the name "collina" on grounds of priority, and united both populations under *B. perpusilla*. The present author is of the opinion, however, that they represent distinct varieties, and accordingly have been reinstated as such.

A particularly interesting collection of specimens was found in a folder at the National Herbarium, Sydney. These specimens were collected at Boulder, and being closely intermixed, were apparently growing and pressed together. They consisted of *B. glandulosa*, *B. perpusilla* var. *tenella*, and a few specimens which had the habit and indumentum of *B. glandulosa*, while the fruit were of the *B. perpusilla* type except that the wing was shallowly dissected, and the glandular hair at the apex of each lobe was abnormally long. Their appearance is very suggestive of hybridization between the two first named species.

Brachycome Clementii Domin. Biblioth. Bot., 89 (1929), 1208.

(Original description. Trans. ex Latin.) An erect annual herb, 15-25 cm. high, slightly or more often much branched and corymbose, the lower portion bearing white, rather rough, scattered hairs. Stems leafy. Radical leaves absent, cauline leaves obovate, either linear-oblongate or more often narrow-cuneate. Lower leaves petiolate, all the rest sessile and acute or coarsely serrate distally, 1.5-6 cm. long, soft, sometimes glabrous. Upper leaves smaller, linear and entire. *Peduncles* slender, short. *Capitula* very dense, hemispherical, about 6 mm. diameter, excluding the rays. *Involucral bracts* equalling the disc florets, linear-lanceolate, sub-acuminate, pilose. *Ray florets* ligulate, very numerous, white, female; rays smooth, obtuse. *Fruit* compressed almost obtriangular, about 1.75 mm. long, pilose, with a narrow wing bearing dense plumose cilia marginally. Pappus reduced, of rigid densely ciliate bristles, one-third the length of the fruit.

North-west Australia, between Ashburton and De Grey Rivers, E. Clement.

From the above description there seems no doubt that this is actually *B. cheilocarpa*, but until syntype specimens are traced and examined Domin's specific name is retained.

ORIGIN AND AFFINITIES.

Until a comprehensive study of allied genera is undertaken, the affinities of *Brachycome* can only be discussed in a general manner. The author is of the opinion that the genera *Bellis*, *Astranthium* and *Brachycome* originated from a common ancestor, and that their present distribution can be satisfactorily explained on Wegener's Theory of Drifting Continents. It is suggested that the common ancestors had a widespread distribution in the northern land mass, and that when the present continents of America and Europe drifted apart and were finally separated the two isolated populations of "probellis", by isolation, became generically distinct. As a result, *Bellis* is confined to Europe and *Astranthium* to America. According to Wegener¹ and Du Toit,² the last land connection between Australia and any other land mass was with South America, through Sub-Antarctica. This, then, would have been the path of migration of the stock which, again in isolation, following the breakage of the subantarctic connection, gave rise to Australasian Genus *Brachycome*. In this connection, the record of a species (*B. Papuana*

¹ Wegener, A.: "Origin of Continents and Oceans", 1924, London.

² Du Toit, A. L.: "Our Wandering Continents", 1937, London.

Mattf.) from the highlands of New Guinea is of particular interest on account of the proximity to "Wallace's Line", which represents an effective natural barrier to the migration of so many plants and animals. Unfortunately it has not been possible to trace any specimens of *B. Papuana* and the possibility of the original specimens having been misidentified cannot be excluded.* An examination of five species of *Bellis* (*B. perenne* L., *B. sylvestris* Cyr. var. *pappulosa* Boiss., *B. coerulescens* Cass., *B. microcephala* Lge. var. *Donatiana*, *B. Natalis-Jesu* Seun. and Maroc.), and a single specimen of *Astranthium* (*A. integrifolium* (Michx.) Nutt.), indicates that *Brachycome* is more closely allied to the latter genus than to the former. The involucre bracts of *Astranthium* have scarious margins, and the fruit closely resembles that of *Brachycome*. This similarity is to be expected on the above hypothesis since these two genera have diverged much more recently than they did from the ancestral *Bellis*.

Inter-specific Affinities.

In all species examined of *Bellis* and *Astranthium* it was found that the connective of the anther was continued beyond the level of the pollen sacs into a distinct appendage. This condition is taken to be the primitive one. In *Brachycome*, however, the species fall into two discontinuous groups (subgenera) on the presence or absence of the anther appendage, the subgenus *Eubrachycome* being the most closely related to the ancestral condition. It is suggested that this genus reached Australia through Sub-Antarctica prior to late Jurassic times when New Zealand was still connected to the mainland of Australia, and consequently would have received its complement of the Ancestral *Brachycome* stock. All the present-day New Zealand species belong to the subgenus *Eubrachycome*, which is to be expected if the mutation which gave rise to subgenus *Metabrachycome* established itself after New Zealand had separated from Australia. Sufficient time has elapsed since the late Jurassic to permit independent speciation in both countries.

Although it is not expected that any species has descended unchanged since Tertiary times, it is realized that certain primitive characters are retained in most groups, evolution never affecting all characters to the same extent at the same time. For this reason certain different evolutionary tendencies† are observed in different lines of descent, and it is proposed to discuss these under the headings of the separate groups.

SUB-GENUS EUBRACHYCOME. (Fig. 123.)

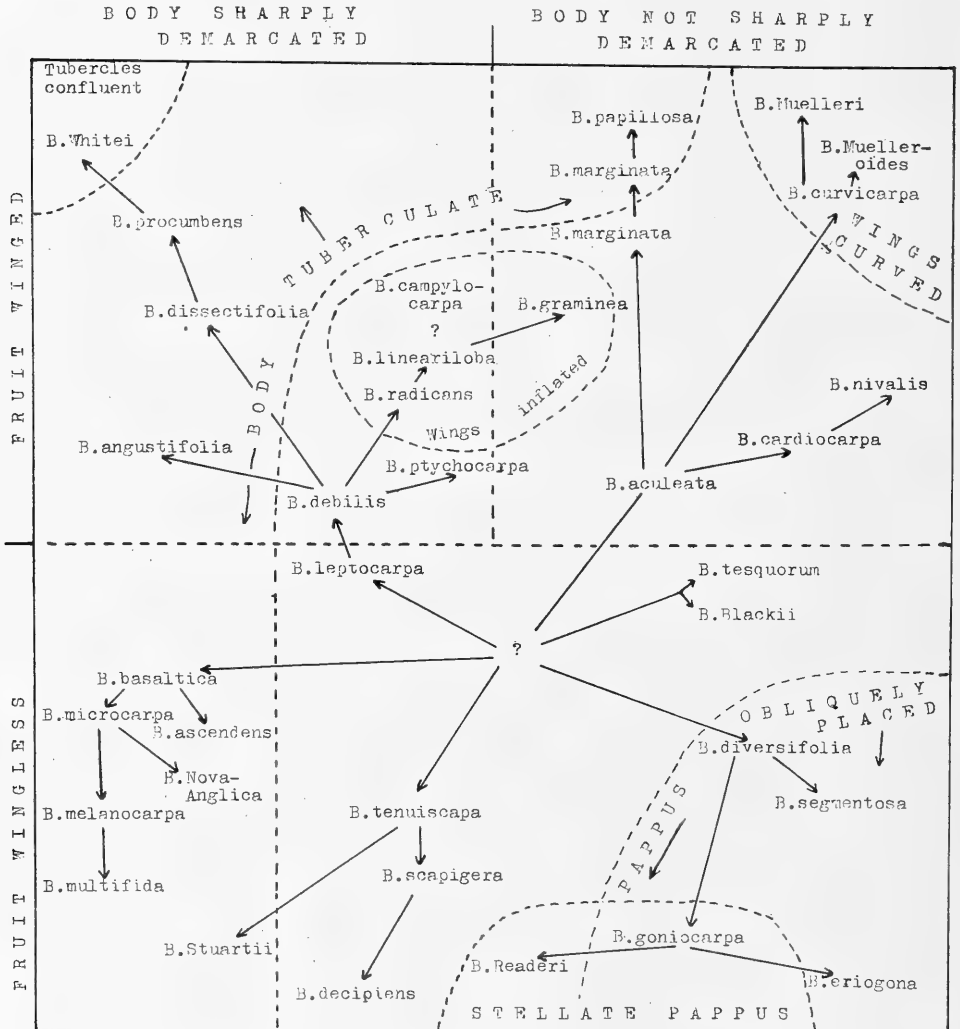
Three major trends are apparent within this group:

- (1) Flattened fruits precede thick ones, which in turn precede those such as *B. goniocarpa* and *B. diversifolia* with an obliquely placed pappus and only one plane of symmetry.

* Two specimens of *B. Papuana* have since come to hand from the Brisbane Herbarium, collected at Saruwaged (10,000 ft.) by C. E. Lane Poole. Unfortunately the fruit are very immature, but they are undoubtedly specimens of *Brachycome*, subgenus *Eubrachycome*.

† G. F. Ferris ("On Certain Evolutionary Tendencies in the Heads of Insects", *Micro-entomology*, ix, Pt. 2 (1944), 78): "Evolution is not primarily the modification of the soma. It is primarily the modification of the genetic materials which produce that soma. Consequently evolution can proceed only on the basis of changes which the genetic materials can offer through the soma to the environment for subsequent elimination or preservation. And what is offered is entirely dependent upon the capacities of the genetic materials themselves. Within these materials there are patterns which are subject to change, but also limit the direction within which change can proceed. To the degree that these capacities are in any way either limited or increased by preceding changes so that the direction of further change is restricted or encouraged, evolution would appear to be determinative. If, in the course of evolution of any group, there is established a genetic pattern which is favourable to or especially susceptible to changes in some particular direction, even though the changes may not appear in the soma of all possessors of the pattern, the results might appear to the observer to recur with such frequency as to require some word by which to express a realization of the phenomenon involved. For this word 'tendency' lends itself. An evolutionary tendency implies the existence of a genetic pattern and of genetic capacities which are favourable to or unstable in the direction of changes that express themselves recurrently, but perhaps irregularly, in the somatic structure of all organisms which possess that pattern and those capacities."

- (2) The presence of distally rolled hairs on the body is a derived condition from glabrous fruit, and both in ontogeny and phylogeny these curled hairs may give rise to tubercles. The position of tubercles in mature condition is fixed by the position of the rolled hairs in the young fruit, and the hair usually persists at the apex of the tubercle. The degree of development of the tubercles is a further trend, reaching an apparent climax in *B. Whitei*, where they became confluent.
- (3) A broad wing is a highly specialized development of wingless fruit by steps including a thickened margin, longitudinal marginal folds and finally the cutting off of a narrow lateral strip of tissue.



Text-figure 123.—Diagram to illustrate affinities and evolutionary trends in subgenus *Eubrachycome*.

In this group the actual size of the pappus is not consistent with other structural trends noted, though it is probable that in the primitive condition it was small.

By a combination of the above primitive characters it is suggested that the hypothetical *Brachycome* ancestor which colonized Australia bore smooth flattened wingless fruits not unlike those of *Astranthium*. In Figure 123 an attempt has been made to express diagrammatically the major orthogenetic tendencies.

Superspecies tenuiscapa.

Component species: B. tenuiscapa, B. Stuartii, B. scapigera, B. decipiens.

In the simple nature of the fruit this group approximates more closely to the hypothetical ancestral form than any other. The component species are very similar in fruit structure, and the discontinuities between them are small, though definite. A general increase in size of the fruit is apparent, reaching a maximum in *B. decipiens*, the fruit of which shows a new character, the presence of straight hairs. *B. Stuartii* bears fruit which in colour and size resemble those of *B. tenuiscapa*. Since it is rare for an orthogenetic trend to be reversed, this suggests that *B. Stuartii* had an independent origin.

The main interest of this group lies in the fact that the fruit can be arranged in a series indicating the possible evolution of the wing of more specialized species. The fruit of *B. tenuiscapa* and *B. scapigera* agree in the possession of a narrow, smooth, slightly thickened margin. In *B. decipiens* this condition is retained, but in addition a narrow longitudinal groove can be seen at the outer edge of the margin on both sides. The presence of these grooves cuts off a lateral strip of tissue which runs down the outer edge on each side of the fruit. The condition seen in *B. Stuartii* is arrived at by the thickening of this very narrow longitudinal strip of tissue into a conspicuous border which has resulted in the longitudinal grooves occupying an apparently more central area. At the same time, the central region has slightly thickened and tends to extend past the grooves. In the present author's opinion the marginal strip of tissue is the morphological forerunner of the true wing, and the central area that of the sharply circumscribed body of the superspecies *leptocarpa*.

Superspecies leptocarpa.

Component species: B. leptocarpa, B. debilis, B. angustifolia, B. dissectifolia, B. procumbens, B. Whitei, B. ptychocarpa, B. radicans, B. lineariloba, B. graminea, B. campylocarpa.

The major tendency in this group is an almost immediate departure from the wingless condition of *B. leptocarpa* to the winged one. Two secondary lines of descent are apparent leading to the development of either thin or inflated wings, while the sharply defined body of the fruit is retained. This tendency towards the inflation of the wings is unique and has already been commented on under the species concerned. A series can be traced from *B. radicans* to *B. graminea* leading to the complete enclosure of the body by the greatly inflated and spongy wings. The exact position of *B. campylocarpa* is not quite clear, but it would seem that a further tendency is here expressing itself in the hardening of the swollen wing into a thick structure while the clearly demarcated "lineariloba" form of the body is retained. It has already been noted that tubercles on the fruit appear to be preceded by curled hairs, so that from *B. leptocarpa* two tendencies can be traced, one of which leads to the complete elimination of the hairs, and the other to increasingly tuberculate fruit. The climax of the latter line of descent is reached in *B. Whitei* where the tubercles have fused and present a somewhat bladder-like structure on each face. The apices of the original curled hairs still persist and mark the position of the individual tubercles.

Superspecies basaltica.

Component species: B. basaltica, B. ascendens, B. microcarpa, B. Nova-Anglica, B. melanocarpa, B. multifida.

This group is characterized by the possession of thick tuberculate fruit with a relatively large pappus. The main tendency is for an increase in number and size of the tubercles and loss of the flattened shape. In *B. melanocarpa* the fruits are occasionally cylindrical and the smooth margins are no longer apparent, the tubercles extending right round the fruit. There is a constant increase in size of the pappus from *B. basaltica* to *B. melanocarpa* where it is a conspicuous structure, and a grouping of the bristles into bundles gives rise to the condition seen in *B. multifida*. *B. Nova-Anglica* agrees very closely with *B. microcarpa* except for the larger size of the fruit and great reduction

of the pappus. The fact that it is localized in its range suggests that it has had a comparatively recent origin. The relationships of *B. ascendens* are debatable in that the fruits show considerable flattening, while the margin is relatively broad and bears irregular tubercles along its edge. The tubercles on the central region are similar to those on *B. microcarpa*, from which species it is thought *B. ascendens* took its origin.

Superspecies aculeata.

Component species: *B. aculeata*, *B. marginata*, *B. papillosa*, *B. curvicarpa*, *B. Muellerei*, *B. Muelleroides*, *B. cardiocarpa*, *B. nivalis*.

All the species are characterized by the possession of relatively large flat fruits with an oval body which is not sharply demarcated from the wing. *B. aculeata* itself is a large and variable species the fruits of which vary in the nature of the wing, which may be almost entire or partially dissected. From this type of fruit it is easy to trace three lines of descent, one leading to the *B. marginata* type with completely dissected wings and more or less tuberculate fruits. *B. aculeata* bears small glandular hairs on the body and it is interesting to note that some specimens of *B. marginata* are densely tuberculate while others are hardly so at all. It would seem that species formation is taking place within the present group of *B. marginata*, but to attempt to subdivide it at the present stage would be to anticipate evolution. *B. papillosa*, in spite of its entire wing, is readily derived from a tuberculate form of *B. marginata*.

The tendency of the wings of *B. aculeata* to fold inwards is sometimes noted, but there is a strong orthogenetic trend in this direction which involves often a curving of the body as well. This tendency reaches its highest expression in *B. Muellerei* and *B. Muelleroides* where the wings after extending laterally for an appreciable distance fold back on themselves and come partially to enclose one face of the body.

Both *B. cardiocarpa* and *B. nivalis* are readily derived from *B. aculeata* by the stabilization of the wing, which in *B. aculeata* is somewhat variable.

Superspecies diversifolia.

Component species: *B. diversifolia*, *B. segmentosa*, *B. goniocarpa*, *B. Readeri*, *B. eriogona*.

This group is very circumscribed and is characterized by the possession of thick fruits bearing a horseshoe-shaped fold on each side. In the case of *B. goniocarpa* the fold is broken up transversely into large and irregular masses of tissue. Two tendencies are apparent within the superspecies, one of which is expressed in an obliquely placed pappus, the other in the development of a stellate pappus. Both these trends are seen in *B. goniocarpa* and *B. eriogona*. *B. Readeri* is obviously very closely related to *B. goniocarpa* and it is thought that its centrally placed pappus has a secondary origin and is not to be regarded as a primitive feature.

Superspecies tesquorum.

Component species: *B. tesquorum*, *B. Blackii*.

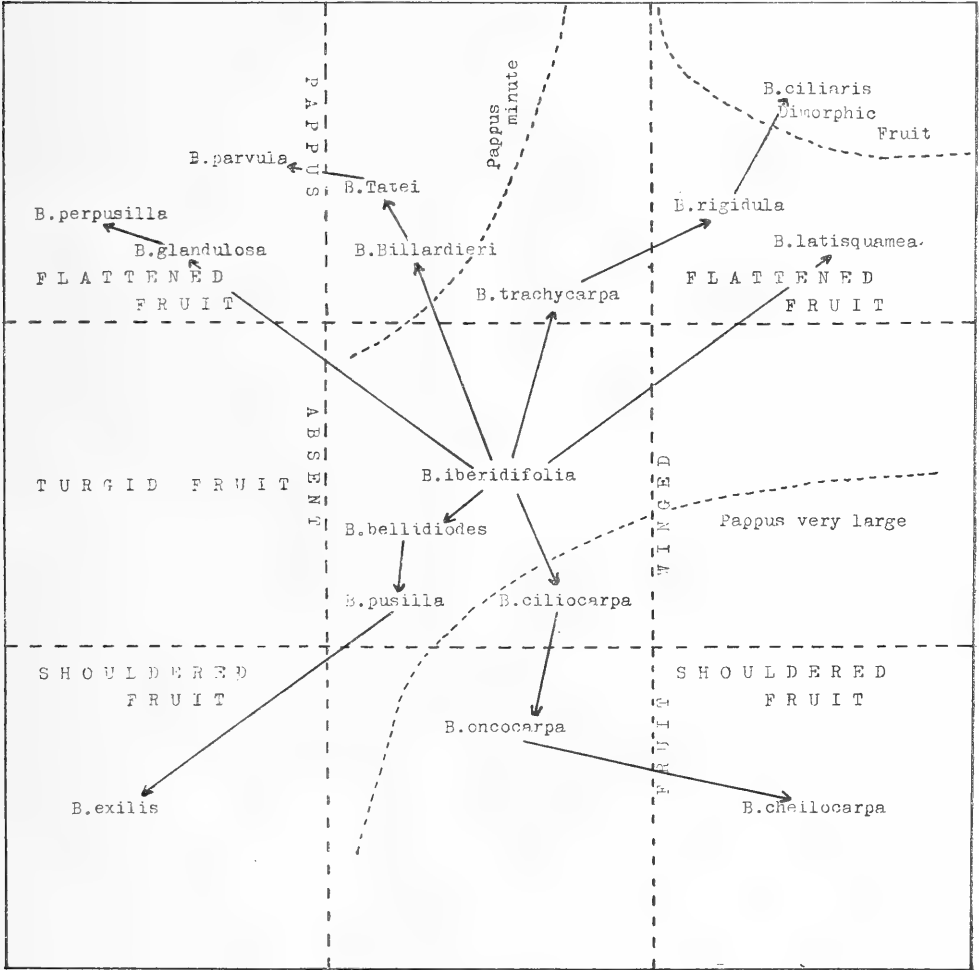
The affinities between these two species is obscure, as is the origin of the group itself. Unfortunately few specimens have been collected, and it is possible that the most striking feature of the fruit, the numerous scattered glandular hairs, is only a character of immaturity. Further specimens bearing undoubtedly mature fruit will do much to clarify the position of these two species.

Subgenus METABRACHYCOME. (Fig. 124.)

Although the possibility of a polyspecific origin for this group cannot be excluded, the author is of the opinion that this predominantly Western Australian subgenus represents various lines of descent from a single ancestral species with the chief diagnostic character of subgenus *Eubrachycome*.

The complete absence of any species of this subgenus from New Zealand has already been noted, and lends support to the argument outlined above that it originated after New Zealand had become separated from Australia, so that migration there was impossible.

Since this group appears to be of more recent origin than subgenus *Eubrachycome* it was considered probable that one existing species may show a maximum number of ancestral characters with the potentialities for specialization in a variety of ways. *B. iberidifolia* is thought to be such a species and is accordingly taken to be the most primitive species in this subgenus. Characters of its fruit such as simple shape, indefinite margin and unstable nature of the pappus are all primitive characters from which the more highly specialized conditions of the other species could readily be derived.



Text-figure 124.—Diagram to illustrate affinities and evolutionary trends in subgenus *Metabrachycome*.

The main orthogenetic trends noted are:

- (1) Towards a stabilization of the shape of the fruit by means of flattening or the development of characteristic "shoulders".
- (2) Stabilization of the pappus by its complete suppression or great enlargement.

Other tendencies are seen in individual superspecies leading to the development of winged fruit, tubercles and glandular hairs. An attempt has been made to express these trends diagrammatically in Figure 124.

Superspecies iberidifolia.

Component species: *B. iberidifolia*, *B. bellidioides*, *B. pusilla*, *B. exilis*, *B. Billardieri*, *B. Tatei*, *B. parvula*.

Two lines of descent are apparent which can be traced from the basal species, *B. iberidifolia*, in each of which the tendency to reduction and finally complete suppression of the pappus is apparent. One of these lines leads to the thick shouldered fruit of *B. exilis*, a condition foreshadowed in *B. pusilla*, the other culminating in the flat fruit with margin of *B. parvula*. *B. Tatei* occupies a position intermediate between *B. iberidifolia* and *B. parvula* structurally as well as geographically, in that the pappus is much reduced, and the margin, though broad, is not wing-like and simply represents an exaggerated condition of that of *B. iberidifolia*.

Superspecies trachycarpa.

Component species: *B. trachycarpa*, *B. rigidula*, *B. ciliaris*.

The predominating trend in this group is towards extreme flattening of the fruit. *B. trachycarpa* can readily be derived from *B. iberidifolia* by the stabilization of the pappus to form a minute crown, and by the development of more or less closely placed tubercles on each face, the margins remaining smooth. It is this type of fruit which is retained by the ray florets of *B. ciliaris*, but in the disc florets the margins have given place to a more or less dissected wing and the tubercles on the body of the fruit have been lost or are only represented by apically rolled hairs. *B. rigidula* and *B. ciliaris* may have been derived independently from *B. trachycarpa* or the former have given rise to *B. ciliaris* as a geographic subspecies. In view of the distribution of these two species the latter origin seems more likely. In this group the habit and pinnatisect cauline leaves of *B. iberidifolia* are retained.

Superspecies ciliocarpa.

Component species: *B. ciliocarpa*, *B. oncocarpa*, *B. cheilocarpa*.

These species bear highly specialized fruits of progressive complexity, and the pappus in each is made up of long bristles. The general shape of the fruit of *B. ciliocarpa* is similar to that of *B. iberidifolia*, though considerably larger, and long apically rolled hairs are present marginally and on each lateral face. The trend towards shouldered fruit becomes apparent in *B. oncocarpa* and is the essential difference between this species and *B. ciliocarpa*. In *B. cheilocarpa* the shoulders are retained, but the margins are greatly enlarged and form more or less dissected wings, while the long hairs on each face have given place to tubercles.

Vegetatively there is strong similarity between these three species, all of which branch from the base and bear mainly radical leaves.

Superspecies latisquamea.

Brachycome latisquamea shows no definite affinity with any other species, and its phylogenetic position in the subgenus is obscure. This is the only species which has woody stems, and attains an almost shrub-like habit. The fruits are very large, and apart from the wing possess no characters such as hairs or tubercles which would indicate its affinities. The lack of these features suggests a distant relationship with the super-species *Silphiosperma*, but beyond that no suggestions can be put forward.

Superspecies Silphiosperma.

Component species: *B. glandulosa*, *B. perpusilla*.

Quite distinct from other members of the genus and further work may justify their being reinstated to full generic status. Although superficially the fruit of one species has the appearance of being winged, the present author is of the opinion that the structure is morphologically the dissected margin.

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DESCRIPTION OF PLATES.

PLATE VI.

Maps 1-32.—Maps showing distribution of *Brachycome* species.

- Map 1. *B. tenuiscapa* var. *tenuiscapa* (X) and var. *pubescens* (●).
- Map 2. *B. scapigera*.
- Map 3. *B. decipiens*.
- Map 4. *B. Sturtii*.
- Map 5. *B. leptocarpa*.
- Map 6. *B. debilis* (X) and *B. ptychocarpa* (●).
- Map 7. *B. angustifolia* var. *angustifolia* (X), and var. *heterophylla* (●).
- Map 8. *B. dissectifolia* (X), *B. procumbens* (●); *B. Whitei* (/).
- Map 9. *B. radicans*.
- Map 10. *B. lineariloba*.
- Map 11. *B. graminea*.
- Map 12. *B. campylocarpa*.
- Map 13. *B. basaltica* var. *basaltica* (X), and var. *gracilis* (●).
- Map 14. *B. ascendens*.
- Map 15. *B. microcarpa* (X); *B. Nova-Anglica* (/); *B. melanocarpa* (●).
- Map 16. *B. multifida* var. *multifida* (X); var. *dilatata* (●).
- Map 17. *B. aculeata*.
- Map 18. *B. marginata* var. *marginata* (X), and var. *chrysoglossa* (●).
- Map 19. *B. papillosa* (X); *B. curvicarpa* (●).
- Map 20. *B. Muelleri* (X); *B. Muelleroides* (●).
- Map 21. *B. cardiocarpa* (X); *B. nivalis* var. *nivalis* (●); and var. *alpina* (/).
- Map 22. *B. diversifolia* var. *diversifolia* (X), var. *maritima* (/), and var. *dissecta* (/).
- Map 23. *B. goniocarpa*.
- Map 24. *B. longiscapa* (X); *B. eriogona* (Δ); *B. tesquorum* (●); *B. Blackii* (/).
- Map 25. *B. iberidifolia*.
- Map 26. *B. Tatei* (X), *B. parvula* var. *parvula* (●), and var. *lissocarpa* (/).
- Map 27. *B. bellidioides* (X); *B. pusilla* (●); and *B. exilis* (/).
- Map 28. *B. trachycarpa* (X); *B. rigidula* (●).
- Map 29. *B. ciliaris* var. *ciliaris* (X), var. *lanuginosa* (●), var. *subintegrifolia* (/), and var. *lyrifolia* (Δ).
- Map 30. *B. ciliocarpa* (X); *B. oncocarpa* (●).
- Map 31. *B. cheilocarpa* (X); *B. latisquamea* (●).
- Map 32. *B. glandulosa* (X); *B. perpusilla* var. *perpusilla* (●), and var. *tenella* (/).

PLATE VII.

1. *B. scapigera* (Lectotype).
2. *B. angustifolia* (Lectotype and Lectoparatype of *B. linearifolia*).

PLATE VIII.

1. *B. lineariloba* (Lectotype and Lectoparatype).
2. *B. diversifolia* var. *diversifolia* (Lectotype of *Steiroglossa humilis*).

PLATE IX.

1. *B. multifida* var. *multifida* (Lectotype and Lectoparatype).
2. *B. aculeata* (Lectotype of *B. Sieberi* var. *Gunnii*).

PLATE X.

1. *B. aculeata* (Lectotype).
2. *B. aculeata* (Lectotype of *B. scapiformis* var. *puberula*).

PLATE XI.

1. *B. rigidula* (Lectotype).
2. *B. ciliaris* var. *ciliaris* (Lectotype).

PLATE XII.

B. graminea (Lectotype). Pl. Nov. Holl. ii, t. 204.

PLATE XIII.

B. exilis (Lectotype).

CARL ADOLPH SUSSMILCH.
1875-1946.

(*Memorial Series, No. 12.**)

(With portrait, Plate xiv.)

It is interesting to note how certain unexpected happenings impress themselves indelibly upon one's memory. Among such "bolts out of the blue" experienced by the writer may be mentioned two impromptu introductions to important personalities. One was the meeting, during 1924, with F. G. Clapp, of lamented memory, in wild, unpopulated North-west Australia, the other, about fifty years since, being the chance meeting with C. A. Sussmilch along an unfrequented trail in a mountainous area about two hundred miles west of Sydney.

Engaged as I was, at the time, in the conduct of a geological reconnaissance of that area, I was surprised to note the approach of a person on the rough track I was following. It was evident that the figure was not that of the ordinary countryman, for he was decked out in proper field boots, leggings, belt, and so on, with maps, hammer, clinometer, and all the usual technical armament which distinguishes the field geologist. Here evidently was a brother of the Hammer. The spirit moved me, as the Apostle Philip relates of himself, on catching sight of the puzzled Ethiopian in the chariot, "Go, join thyself to this man". "Mr. Sussmilch, I believe", said I. "And you are friend Andrews, I think", said he. Thus commenced a friendship only terminated by his passing away on 8th December, 1946.

Sussmilch was born in Sydney, New South Wales, on February 12th, 1875. His father was Christian Bernhardt Sussmilch, a native of Hamburg, Germany. He had taken residence in Sydney while yet a mere youth. In his new homeland he taught music for a living. Here in Australia he met and married Anne Emilie Merkle, who became Carl's mother. Her mother, in turn, had been born in Heilbronn, Württemberg, Germany, and she had arrived in Sydney as a widow with Sussmilch's mother as an infant in arms, the father having died on circuit in his office as judge, the infant not having been born until six months later. Sussmilch's mother thus, to all apparent intents and purposes, was an Australian, and the father was a naturalized British subject.

Six children were born to the pair. All were musical and several attained prominent positions in the musical centre of Sydney. Mrs. Con Jones, of Vancouver, Canada, is the eldest, and she had been a member of the Royal Philharmonic Society of Sydney. William, the second child, was a fine violinist, and for many years was leader of the second violins in the Sydney Orchestra. Carl Adolph, the subject of this memorial, was the third child. The fourth was Emma (Mrs. Allard), who achieved public recognition as a singer. She studied for three years at the Berlin Conservatory, and was the first scholar outside of Germany itself to win the Charlottenberg Scholarship. Emil, the fifth child, was an officer in the Registrar-General's Department, Sydney. He was a recognized singer among the artists in Australia. Sussmilch himself remained unmarried, but prepared a home for the family, of which Marie, the youngest child, took charge.

Sussmilch attended the State Public School at William Street, Sydney. His early efforts at earning a living consisted of various indenting activities. While so engaged

* By E. C. Andrews. The writer gratefully acknowledges the information supplied by the family of Mr. Sussmilch, by Mr. P. D. Riddell, Director, Technical Education, N. S. Wales, W. G. Stone, Chief Chemist, Geological Survey, N. S. Wales. The Bibliography was supplied by Dr. G. D. Osborne, Geological Department, Sydney University.

he attended classes at the Sydney Technical College. At a still later stage he attended courses of lectures given at Sydney University, gaining honours at the final examinations in Geology, Mining, and Metallurgy.

In 1900 he was appointed to the Sydney Technical College as an assistant in the Department of Geology and Mineralogy. Then, in 1903, came promotion to the position of teacher in that institution, and, in 1908, the Department of Education appointed him to the position of Lecturer in Charge of Geology, Mineralogy, and Mining in the College.

In 1914 he became Principal of the Newcastle Technical College. Thus, in great measure, scientific pursuits necessarily gave place to administrative duties. This position he retained until 1927, when he was appointed Principal of the East Sydney Technical College and Assistant Superintendent of Technical Education. In 1934 he became Acting Superintendent of Technical Education, a position which he vacated in 1936 to enable him to conduct private research work in geology and geography.

Sussmilch joined various scientific and civic institutions, and undertook extensive travel to assist him in broadening and intensifying his scientific, educational, and philanthropic activities. This memorial deals mainly with him as a scientist and colleague; nevertheless he is better known to many of his friends as an educationist and philanthropist. He was a skilled and successful educationist, a man of direct method and marked punctuality, but above all a man of broad human sympathies.

Through the courtesy of the New South Wales Society for Crippled Children I am indebted for the following:

"Mr. Sussmilch was Chairman of the Board of Directors in April, 1931, and was, at the same time, appointed to our Educational and Vocational Guidance Committee. He served in these capacities until the 6th February, 1940, when he was also appointed Honorary Secretary to the Society, from which position he resigned on the 16th September, 1943, due to ill health. At the same time he resigned also from the Board, and had very little contact with our Association from then until his death.

"Mr. Sussmilch made a splendid contribution to the rehabilitation of physically handicapped children through the Educational and Vocational Guidance Committee, and his personal interest in the young people who came before him was of extreme value to our work. Mr. Sussmilch, in his capacity as Chairman of this Committee, was able to utilize his knowledge of educational facilities and his experience, gained while employed as Director of Technical Education in the Newcastle District. One of the Society's functions is to advise young people prior to, and at, school-leaving age, according to their ability, and to arrange vocational training as need arises. The responsibility for this falls to the Chairman of the Educational Committee, and a great many young people satisfactorily employed at present owe their success to Mr. Sussmilch.

"As Honorary Secretary of the Society his knowledge of Committee work and his long association with the Board of Directors proved a valuable asset."

Mr. Sussmilch's pioneer work as one of the important Committee on Science House Management (Science House is a successful endeavour to house the main scientific societies of Sydney in one building) is but another evidence of his energetic and valuable civic activities.

Sussmilch's eminence as a teacher appeared to arise from his lucid, unambiguous, and direct statements concerning scientific subjects; his success also owed much to his unswerving punctuality in keeping appointments and in observing faithfully the times for delivering lectures. As a teacher, moreover, he sought to inspire his students and the public with a love for geology and a robust spirit of comradeship and citizenship. To assist him in public speaking he subjected himself to a rigorous course of training in elocution and general speaking. It is now more than thirty years since that the writer sought to understand the origin of his lucid style, his persuasive manner of lecturing, free from stammering, repetition, posturing, and other mannerisms. With his usual placid smile he explained that it was gained under the relentless battery of severe personal criticism delivered by a strict teacher of elocution. "Awkwardness, bashfulness, and mannerisms are quickly knocked out of you", he stated, "when the teacher of elocution designates all such bashfulness, nervousness, and so on, as mere expressions of personal vanity and selfishness".

In furtherance of this desire to popularize his lectures, to broaden his own knowledge, and to establish friendly relations with scientists abroad, he undertook extensive travel. On several occasions he visited the United States and Canada, making special geographic inspection of the Canadian Rockies, Yellowstone Park, Crater Lake, Yosemite, the Grand Canyon, together with the local geology of the San Francisco, Chicago, New York, and other areas.

But ever through this devotion to scientific and educational work might be seen peeping out the desire to promote a feeling of international good will. This was exemplified during the meeting, in 1914, of the British Association for the Advancement of Science in Australia, and in his visit, during 1920, to the Hawaiian Islands, to attend the First Pacific Science Congress, called by the scientists of the United States. Together with a number of colleagues from Australia, he replied to the earnest appeal of the United States scientists, made at the Honolulu meeting, to meet together triennially at various countries in the Pacific region with the idea of promoting harmonious social relations among the various peoples living within that area. These meetings were continued for years, apparently with great success, and ended suddenly only by the clouding over of the political horizon in the later 1930's, culminating in the World War of 1939. This was a very disappointing ending to twenty years of strenuous work by Pacific scientists to maintain peace within their borders. In passing, it may, however, be shown hereafter to be but a temporary setback, inasmuch as the seeds of a grand harvest of good will have been well sown in various Pacific countries.

Sussmilch's lectures at the Technical College, together with his definite powers of exposition both as a teacher and as a popular lecturer, made a powerful appeal to students and the public alike. His classes were popular and his students were loyalty itself. He had the magnetism of the lucid and enthusiastic expositor; he possessed the respect also accorded to the teacher speaking *ex cathedra*, rather than with the caution of the research student. His lectures were such models of lucidity, delivered with such conviction, that many of his students appeared to class geology as one of the exact sciences.

Perhaps it was his annual excursions into the field which attained the height of popularity with the students. These excursions were undertaken to well-known mining areas, such as the Cobar copper field and the main coal province (Permian) of New South Wales, together with areas also of academic geological interest. So popular were these excursions that visitors other than students proper sought to be privileged to attend them, for all knew the unalterable plan of Sussmilch to work to a strict and comfortable time-table. The times of arrival at the site chosen, the times of meals, of leaving and arriving (at home) were all worked out almost with railway time-table precision. At the excursions there was no straggling, not simply because his word was law, but because the students felt attracted to his personality. The writer noted, nearly forty years ago, how his mining students followed him closely during his visits to the various Cobar mines. All were attentive, loyal, and eager to learn.

Naturally, certain interesting happenings are related concerning these excursions. Certain of them, for example, were held in areas traversed by clear mountain streams, and no visit to an area of this type was considered to have been completed satisfactorily unless—as the ancient Greeks and Romans might have been expected to express it—due reverence had been paid to the naiads or nymphs, that is, the lesser tutelary deities of the stream under the general sovereignty of Neptune. The rites observed during the visits to these streams were not as ceremonious or as strenuous as those observed by the Bacchantes and Corybantes in paying reverence to Bacchus and Cybele. The rites accorded to the stream nymphs implied nothing more complicated than scampering and splashing about in the nude in the home of the nymphs.

It was on a certain celebrated excursion, held about forty years ago, approximately, that Sussmilch exhibited personal qualities as leader and colleague in a noteworthy manner, qualities which permitted him to emerge from a difficult situation without loss of dignity, authority, or feeling of comradeship. The geological field work

associated with this particular excursion had been conducted in the heat of a mid-summer day and had been followed by the pilgrimage to the abode of the local naiads. The usual simple water rites were indulged in.

Two senior visitors, however, unaccustomed to the discipline observed by the students, had become separated from the main party, ostensibly in a search for fossils, and only finding their way back to the main party at a time when the members of the latter were indulging merrily in the accustomed Neptunian rites.

It was just at the moment which marked the return of the prodigals that Sussmilch, emergent from the stream and clad merely in a transparency of shimmering moisture and a wreathing smile, stood poised ready to dive preparatory, it would seem, to conducting an examination of the subaqueous geological structures. By the peculiar method known to astronomers as averted vision, his watchful eye had observed the attempt of the prodigals to return by devious and unobtrusive ways to the general congregation. Checking himself suddenly in his projected plunge, he burst into a loud peal of laughter, and, with an accusing finger, drew attention to the stealthy return of the truants. This was too much, however, for one of the discomfited visitors, who responded by taking a flying shot at the leader with a geological specimen, in the form of a handful of slime scooped from a slippery bank. It caught Sussmilch fairly about the equatorial region, spread out from this as a centre, imparting to him a general mottled appearance suggestive partly of that usually ascribed to the Ethiopian and partly to the spots of the leopard. Amazement and dismay were registered plainly on the faces of the students at this ill-timed pleasantry. Sussmilch, however, without a moment's hesitation, and without losing his broad smile, took his deferred dive and reappeared with the same beaming smile, but with no trace remaining of the sooty appearance of the Ethiopian or the spotted nature of the Leopard. His swift action in diving had given the lie to the saying that where mud is thrown some is bound to stick. It was a wholesome lesson to the contrite visitor, who never forgot the incident; it was a lesson also to all in showing how a born teacher can turn even an apparent slight to advantage.

Sussmilch was a true Australian, although possessed of sincere international sympathies. The writer well remembers a chat with him during 1909 while on a geographic excursion. The talk had been on national loyalty. His opinion, definitely expressed (five years prior to World War I), was that a man's loyalty was due really to the country in which he had decided to live. He maintained that there could be no real world peace until international tolerance became general and until jingoistic national flag-flapping should be discontinued. His forebears hailed from Germany, but he had been born in Australia, where he had been encouraged by his parents to speak English (he never learned German), and he declared himself to be Australian.

To colleagues and visiting scientists he was a generous host and friend. He found time also to undertake the honorary secretarial duties of the Royal Society of New South Wales.

In all these honorary activities in the cause of science, education, and citizenship he was absolutely reliable and punctual.

SCIENTIFIC WORK.

Sussmilch carried on much of his original work in geology and geography so as to be enabled to give his classes and the public (by means of popular lectures) the benefit of advances made in these sciences.

Quite early in his field studies he had been impressed with the well-known fact that the Permian sediments of central-eastern New South Wales rested, with marked unconformity, on the folded sediments belonging to the Upper Devonian. He noted also that large granite intrusions of the folded Upper Devonian had not intruded the overlying Permian. From these observations, conducted sixty to one hundred and fifty miles west of Sydney, he was led to refer to the period of movement which affected the Upper Devonian together with the plutonics associated with it as the Kanimbla

Movement, naming it for the Kanimbla Valley in the Blue Mountains, where the effects of this movement are well shown.

The better to spread the general knowledge of the geology of his home State, he prepared a volume on the geology of New South Wales. This octavo volume was published in 1914 with 269 pages, one hundred illustrations, and maps. Years later Sussmilch attempted to issue a later edition of this text-book. But no publisher was found willing to undertake the production with the same excellent class of paper, attractive printing and illustrations. The amount of profit apparently did not appear sufficient to justify local publishers in the outlay of the necessary expense.

It is now about fifty years since the younger geologists of New South Wales became attracted to the more modern methods employed in physiographic research. Sussmilch threw in his lot wholeheartedly with the pioneers of this work in his State. The seniors in geological science in that State viewed the new ideas with evident disfavour, and severe were the criticisms directed at the application of the new ideas to explain the peculiar geographical facts of form presented by the Australian landscapes.

The Geological Section formed by the Royal Society of New South Wales was the meeting ground for the discussions on this and kindred subjects. Very widely divergent opinions were held concerning the origin of the various physiographic facts of form in Australia. The main points on which disagreement was experienced included the duration of the Pleistocene period and the whole theory of peneplanation, with its suggestion of great age, for the various divisions of the Tertiary era.

It was while Sussmilch was in charge of technical training at Newcastle that he was led to study the massive conglomerate and other remarkable deposits of the Carboniferous lying to the north of that city. The nature of these deposits, their contained fossils, and the severe folding to which they had been subjected, suggested that they represented a remnant of important geosynclinal deposits belonging to the Lower Carboniferous.

To the long-extended trough in which these Carboniferous sediments, together with the associated Devonian beds, had been deposited Sussmilch proposed the name The Tasman Geosyncline, while to the large land area from which these sediments appeared to have been derived, but now submerged beneath the sea, he proposed the name Tasmantis.

It was while he was studying this interesting Carboniferous complex that he was led to an important fact connected with Carboniferous climate.

In 1914, at the time of the Australian meeting of the British Association for the Advancement of Science, the base of the "Permo-Carboniferous" in eastern Australia had been accepted as the lower limit of the Lochinvar beds in the Hunter River Valley. In the notes on the geology of the Commonwealth prepared by him for that meeting, T. W. E. David drew attention to the term "Permo-Carboniferous" as being unnecessary, because, in his opinion, the strata lying above the basal Lochinvar beds were considered to be Permian. These Lochinvar beds, it is important to note, contained abundant evidence of glacial remains.

As far back as 1884, Wilkinson had found evidences of glacial action in the Upper Marine Series of the Hunter River area. Oldham, of the Geological Survey of India, had visited the area in 1885 with Wilkinson and had found there an ice-scratched boulder. David's field work had shown that the Lower Marine beds contained even more striking evidence of ice action than the Upper Marine. These beds he named the Lochinvar Glacial Beds, and included them in his Lower Marine stage of the Permian.

Complexity, however, entered into the problem when, at a later date, Sussmilch proved that certain glacial beds in the same district belonged to the Kuttung Series of the Carboniferous. At this stage David collaborated with Sussmilch on the necessity of determining the plane separating the Permian and the Carboniferous. The result was their joint paper in 1920 entitled "Sequence, Glaciation, and Correlation of the Carboniferous Rocks of the Hunter River District in New South Wales".

In this joint publication by Sussmilch and David the plane separating the Permian from the Carboniferous was placed 2,500 feet stratigraphically (approximately) above

what David had formerly named the Lower Marine. The base of the Permian, as thus chosen, consisted of a coarse conglomerate containing abundant remains of *Eurydesma cordatum*.

In 1923, however, David felt compelled to return to his earlier conclusion and placed the plane of separation of Permian and Carboniferous "at the point where, at Lochinvar, the soft shales of the Lower Marine Series (Permian) are replaced by the harder rocks of the Kuttung (Carboniferous)". This was supported by the work of W. R. Browne and W. S. Dun, who, in 1924, found *Eurydesma hobartense* in the Lochinvar shales with these resting directly on the Kuttung.

It was Walkom who, with his knowledge of the *Rhacopteris* and *Glossopteris* floras, was enabled to throw more definite light on the problem. In 1929 he "from comparison of the fossil floras, placed the base of the Permian in the position originally suggested by David, that is, at the base of the Lower Marine Series".

Attention was drawn by Walkom to a point needing careful consideration in matters such as that under discussion, namely, "the greater importance of the first prominent appearance of a new flora (or fauna) in the determination of age than the presence of the last lingering representatives of an earlier one".

In 1931 Sussmilch, with David, proposed to return to their earlier work regarding the plane of separation between Permian and Carboniferous, by reason of the apparent difficulty in reconciling the continuous passage of glacial conditions from Carboniferous into Permian. Walkom's paper, however, indicated a Lower Carboniferous age for the *Rhacopteris* beds and that the Permian "rests directly on Lower Carboniferous".

In 1946 the Committee of the Australian and New Zealand Association for the Advancement of Science on the Correlation of Late Palaeozoic Rocks in Australia (C. A. Sussmilch, chairman) stated that the glacial deposits of the Permian and the Kuttung beds differ widely from each other. "They differ not only in environment and lithology, but the materials of which they are composed were derived from different sources. This point was stressed by Browne and Dun in 1924." This places the base of the Lochinvar as the base of the Permian.

HONOURS.

Sussmilch was appointed Member of Council of the Linnean Society of N. S. Wales, 1933-1946; Member of Council of Royal Society of N.S.W., 1910-1938; President, Linnean Society, 1936-1937; President, Royal Society N.S.W., 1922; President, Newcastle Division, Institution of Engineers, 1920; President, Rotary Club, Newcastle, 1927; Fellow, Sydney Technical College, 1914; Fellow, Australian and New Zealand Association Advancement Science; Member, Australian National Research Council; Chairman, Section C (Geology), 1935, of Australian and New Zealand Association Advancement Science; Member, Board of Trustees, Australian Museum, 1943-1946; Trustee, Australian and New Zealand Advancement Science; Clarke Memorial Medal, Royal Society New South Wales, 1939; Clarke Memorial Lecturer, 1941; Director, N.S.W. Society for Crippled Children, 1932-1943.

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Maps showing distribution of *Brachycome* in Australia



Boite	cm
N° 168	Herb. genevense
	cm

B. linearifolia DC
DE CAND. prod. 5 n° 206 n° 5

(Neotype of
B. linearifolia)

Brachycome linearifolia DC

Syngonium
Barb. & Thibaud

Holl. 11 n° 160 n° 160
1816

(Lectotype of
B. linearifolia)

Boite	cm
N° 182	Herb. genevense
	cm

B. longivista DC
DE CAND. prod. 4 n° 277 n° 12

Senecio longivista Cass. *longivista*
Brachycome DC

El Nov. Holl. No. 532

Senecio longivista

1777 n° 1000 n° 20

Lectotype

2

1

The Genus *Brachycome*.

Lectotype.



Lineariloba DC.
DE CAND. prodr. 6 p. 34 n. 4

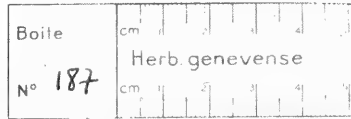
Steiroglossa lineariloba DC.



Herb. genevense
Lectoparatype
Lectotype of Steiroglossa humilis DC.
July 1877

1 Lectoparatype.

Steiroglossa humilis DC.



Humilis DC.
DE CAND. prodr. 6 p. 39 n. 3

(Lectotype of Steiroglossa humilis)

(Lectoparatype of Steiroglossa humilis)

Herb. genevense
Lectoparatype
Lectotype of Steiroglossa humilis DC.
July 1877

2

Brachycome Strobilifera

B. Sieberi DC

Dr. Cassin, prodr. 3 p. 340 t. 4



Boite	cm
N° 178	Herb genevense
	cm

Lectotype
B. Sieberi
var. (var. unguis)

Mr. Sieber 1823

485

2

B. multifida DC

Dr. Cassin, prodr. 5 p. 306 t. 6

Lectotype

Boite	cm
N° 172	Herb genevense
	cm



Brachycome multifida DC

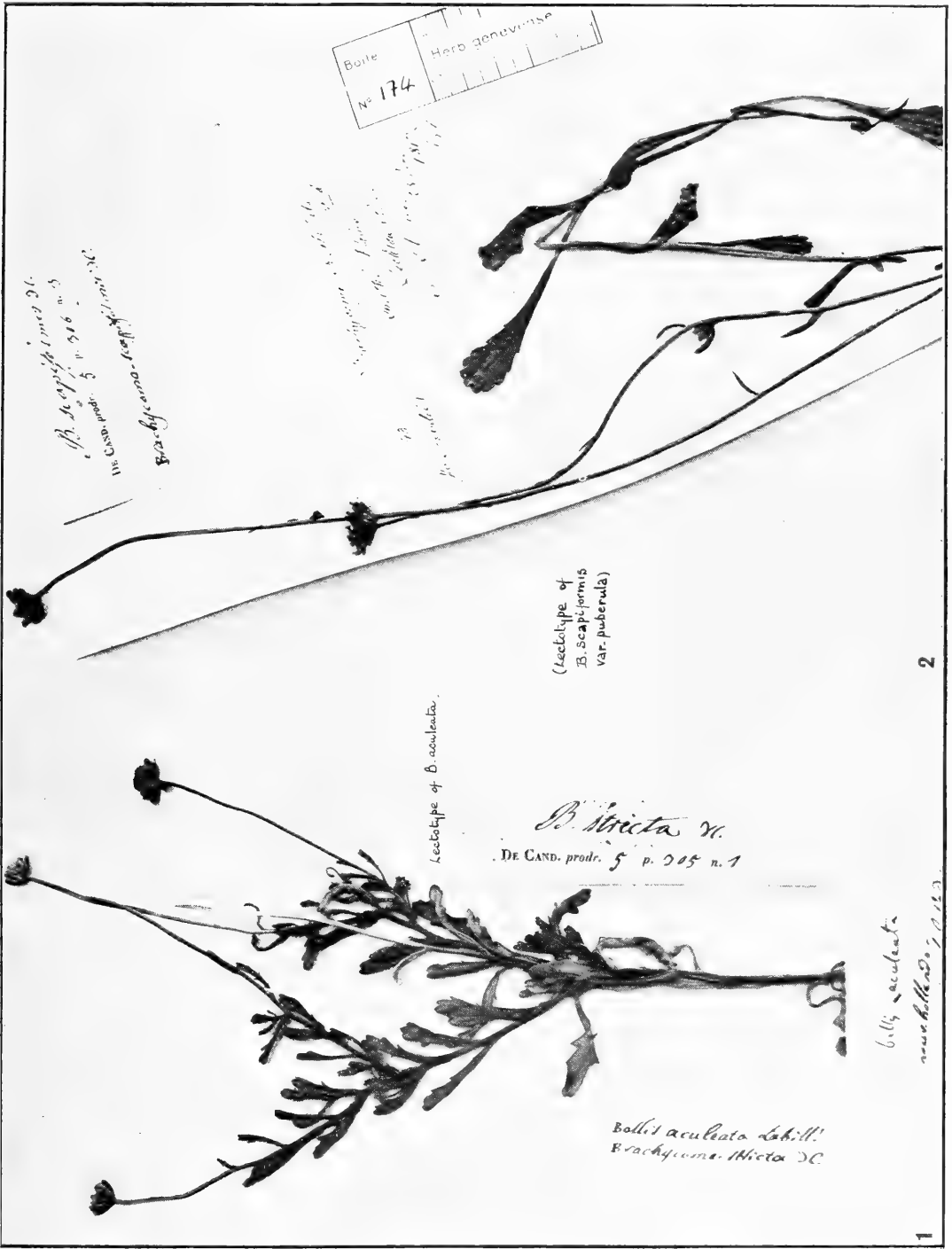
Lectopara type

Brachycome exilis DC
Dr. Cassin, prodr. 5 p. 306 t. 6
Dr. Cassin, prodr. 5 p. 306 t. 6
Dr. Cassin, prodr. 5 p. 306 t. 6

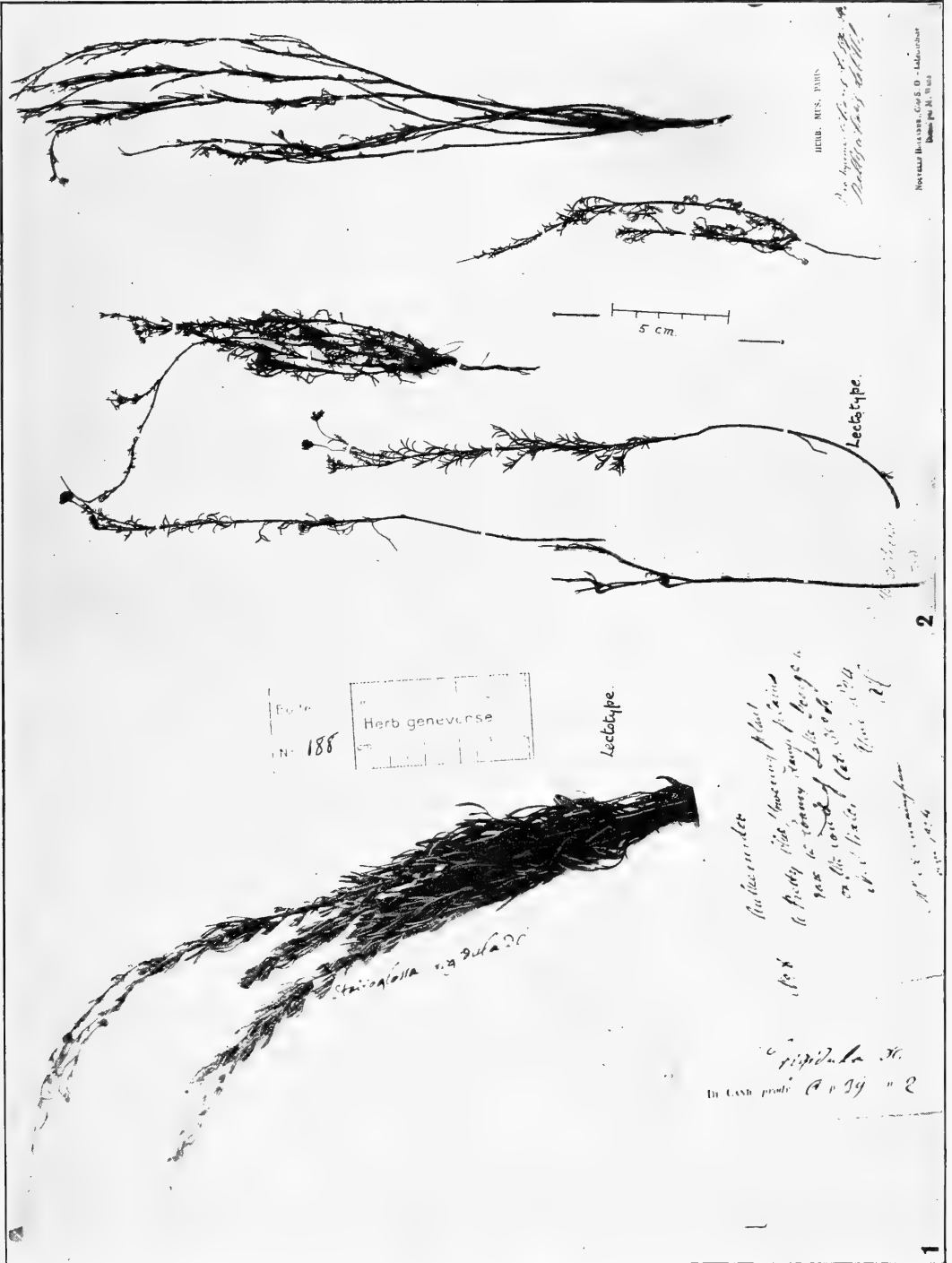
3

1

The Genus *Brachycome*.

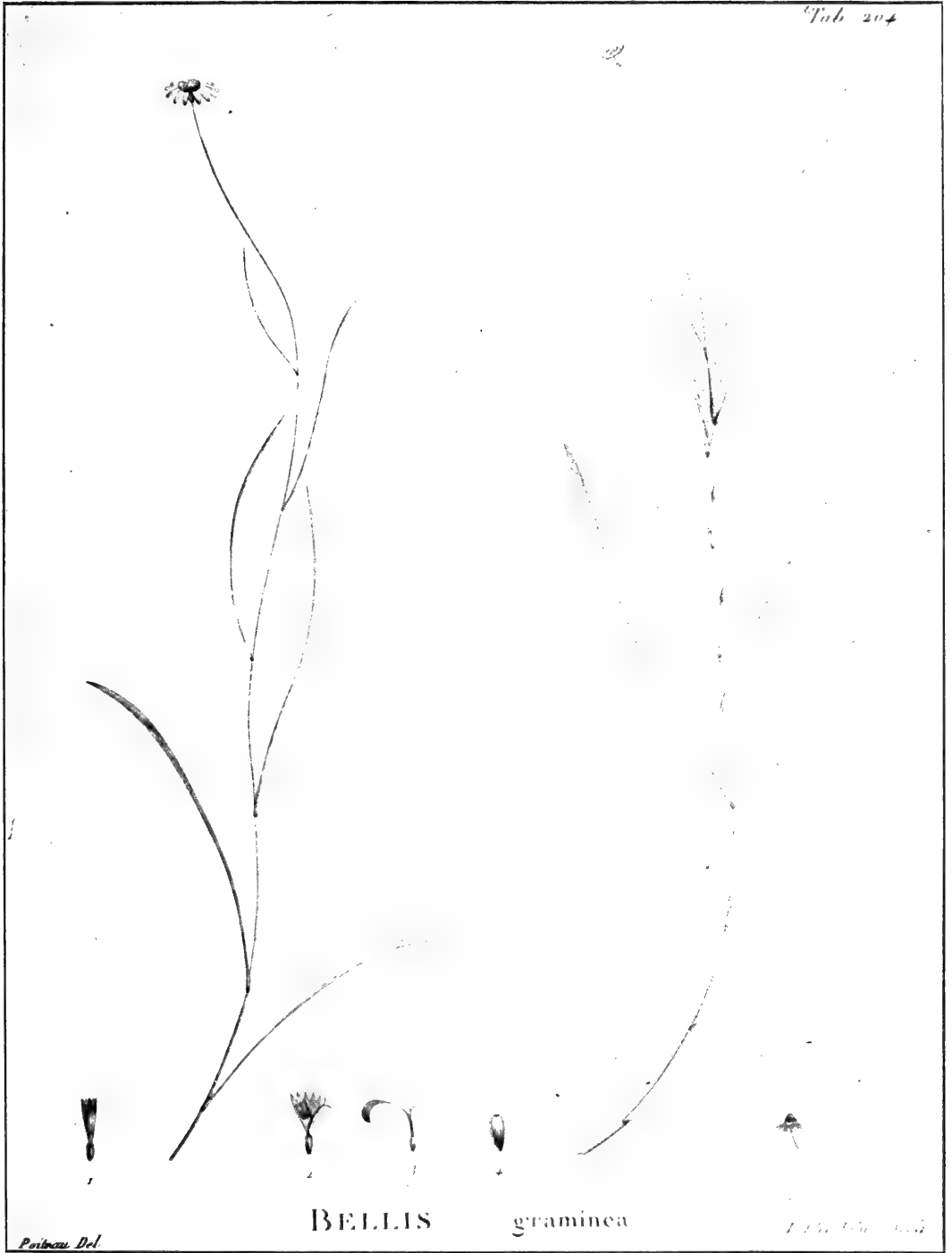


The Genus Brachycome.



The Genus Brachycome.

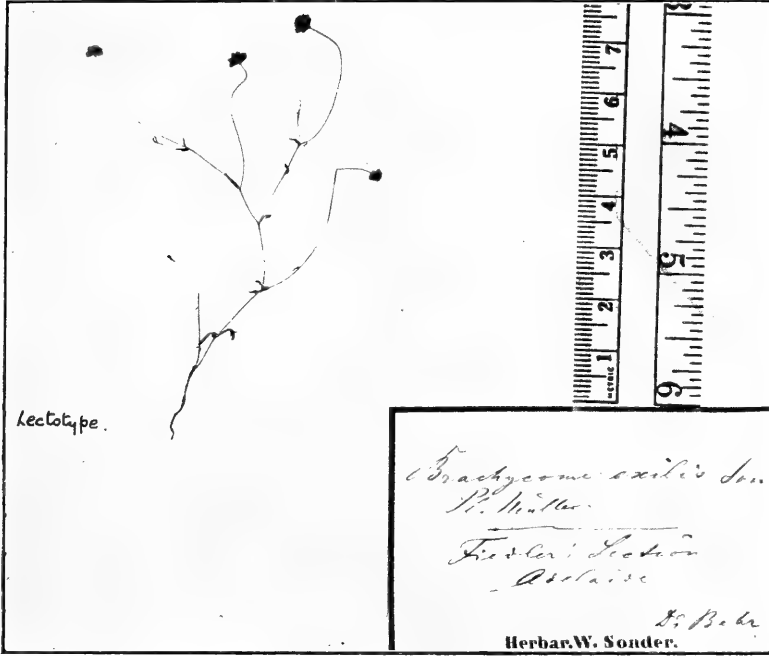
Tab 204



BELLIS

graminea

The Genus *Brachycome*.



The Genus Brachycome.



Carl Adolph Sussmilch.



PRELIMINARY STUDIES ON GUIGNARDIA CITRICARPA, N. SP.: THE
ASCIGEROUS STAGE OF PHOMA CITRICARPA McALP. AND ITS
RELATION TO BLACK SPOT OF CITRUS.

By TEMPLE B. KIELY, B.Sc.Agr.,

Plant Pathologist, N.S.W. Department of Agriculture.
(With Plates xv-xxi and eleven Text-figures.)

[Read 29th September, 1948.]

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INTRODUCTION.

This paper is a preliminary report on some of the more important results of an investigation of the Black Spot disease of citrus on the central coast of New South Wales, carried out at intervals over a period of six years between 1938 and 1948. Epiphytological studies, host-parasite relationships, latent infection studies, the results of experiments aimed at the controlling of the disease and a more detailed discussion of the present subject matter will be the subjects of future papers.

THE DISEASE.

Black Spot is most serious on the Late Valencia orange fruit. However, lemons and grapefruit are affected to a lesser degree under central coastal conditions. Mandarins and navel oranges are affected on the North Coast, where winter conditions are warmer at a time when these two varieties are maturing.

HISTORY AND OCCURRENCE.

The Black Spot disease of citrus was noted officially and described in this country by Benson in 1895. He recorded that heavy losses of oranges had been sustained in the Seven Hills, Castle Hill and Dural citrus-growing areas around Sydney, and that the disease was also serious at Kurrajong, Emu Plains and other unspecified citrus-growing districts. Benson did not study the causal organism, but published drawings of fruit and lesions which are typical of the Black Spot disease as we know it today.

Cobb (1897) gave measurements of spores produced on oranges. The "conidia" ranged from 10μ to 15μ in length and 7μ to 8μ in breadth. Cobb considered the causal fungus was *Colletotrichum adustum* Ellis.

The first detailed description of the causal organism was given by McAlpine (1899). On the structure of the pycnidial form of the fungus occurring in typical lesions on lemon, orange and mandarin fruits, he assigned the organism to the genus *Phoma* and described it as a new species, *Phoma citricarpa* McAlp. He commented that it was

rather surprising that this disease which was so serious and widespread in coastal citrus orchards in New South Wales "should have so long been neglected and its cause not investigated". It is evident from this statement that the disease had been known prior to 1895, when Benson's description was published.

Allen, Blunno, Froggatt and Guthrie (1902) later referred to the causal organism of the disease as *Colletotrichum adustum* Ellis, and observed the impossibility of keeping fruit in store, and the depressing effect of the disease on the market value of affected fruit. Photos were published of typically affected orange fruits. Similar references and illustrations appeared in the "Farmers and Fruitgrowers' Guide" (1904).

Cobb (1904) stated that misconceptions existed about the ability of the disease to spread in the case during storage. Inoculation experiments on ripe lemons indicated that even after one month no success had been obtained. He stated "if it does develop in cases of fruit in store, the disease does so from spots that are already started, but invisible". This is the first recognition of the latent nature of the infection with this particular disease. Cobb recorded the difficulty with which the pycnidiospores may be germinated, and noticed that some spores germinated around air bubbles, as though a high oxygen concentration was necessary. He also stated that on one occasion fructifications of two kinds had been observed—the pycnidia and "the perithecia which are of about the same size, but ascophorous". He did not, however, publish descriptions of this form of the fungus and did not state on what plant parts it was observed.

An experiment confirming the possibility that infection could be latent in apparently unblemished fruit was described in 1909 (Anon, 1909). Six cases of fruit of the 1908 season, some from Narara and some from Dural, were sent to Mr. McAlpine, Government Pathologist, in Melbourne. Half the consignment were clean at the time of packing, the remainder being slightly spotted. The fruit when examined in Melbourne was found to be badly spotted, including those which were unblemished when packed. Of the fruit from Narara, 26% only was saleable, the remainder being badly affected with the disease. This is the first record that the disease occurred on citrus trees in the Gosford, central coastal area.

Darnell-Smith (1916) described results of spraying experiments aimed at the control of the disease, and later (1919) published some observations on the life history of the causal organism. The results of further experiments on control were described by Noble and McCleery (1931).

In an important paper McCleery (1939) gave details of extensive investigations on control methods conducted over fourteen years on the central coast of New South Wales. The latent nature of the disease was confirmed. Evidence was presented that the main infection period probably extended from petal-fall until about twenty weeks later, but the disease on these fruits did not appear until approximately twelve months later. Kiely (1945) recorded an increased susceptibility of fruit to Black Spot with age of tree.

It is not certain how long the disease had been present in the citrus-growing areas of Queensland. Veitch and Simmonds reported the disease in 1929 and made suggestions as to its control.

The first indication that the disease occurred outside Australia was the publication of a paper by Lee (1920) in which the disease was described and the causal organism isolated in pure culture from citrus fruits grown in China in the Canton, Hongkong, Swatow, Amay and Foochow districts. Lee stated the disease did not occur at that time in Japan or the Philippines.

An interception of orange peel imported from China was made by the Commonwealth quarantine authorities in 1920. In reporting this, Birmingham (1924) stated that examination of this revealed the typical lesions of Black Spot and the pycnidial structures and pycnidiospores of *Phoma citricarpa* McAlp. The fruits were reported to have been grown in the Shanghai district. However, this area may have been where the peel was processed and not where the fruit was produced.

The United States Department of Agriculture Plant Quarantine and Control Administration Service (1932) announced that *P. citricarpa* McAlp. had been intercepted on oranges imported into the United States from India, China and Japan. This was the first indication that the disease occurred in Japan or India.

The severity of Black Spot of oranges was stated by Tu (1933) to be increasing in severity in South China, especially on mandarins. Yu (1934) stated that around Nanking Black Spot was widespread and common but caused little market wastage, and Wei (1940) recorded it in the Nanchung area.

A variety of the causal organism was described by Nakata (1934), *Phoma citricarpa* McAlp. var. *mikan* Hara, occurring in certain parts of Japan and Formosa, but Wei (1940) stated that the symptoms and spore size of *P. citricarpa* var. *mikan* Hara were variable factors, dependent on the mode of infection and the nutrient media, and reduced the variety to synonymy with the type species. In Formosa, Sawada (1935) claimed that wounds on the fruit surface inflicted by the insect *Rhynchocoris humeralis* appeared to constitute the principal channel of entry of *P. citricarpa*.

Marchionatto (1928), in a publication dealing with new or little known parasites of the Argentine, recorded the occurrence of *P. citricarpa* McAlp. on lemons in that country. It was later recorded in Brazil by Averna (1937).

P. citricarpa was recorded by Muller for the first time in the Batavia district of Java in 1939. It was stated to have caused appreciable damage to pomelos while the fruit was still hanging in the trees. The lesions were confined to the upper layers of the peel, but after harvesting, both rind and pulp became involved, so that extensive rotting in transit resulted.

Tzereteli and Tchanturia (1939) reported that this disease had developed in storage from citrus fruits grown in the Georgian Socialist Soviet Republic. This was the first record of the disease from the U.S.S.R.

Doidge (1929, 1931) and Doidge and Van de Plank (1936) reported the disease in South Africa from the Pietermaritzburg mist-belt area. Doidge (1929) commented that at that time this fungus had been recorded only in Australia and China.

The United States Department of Agriculture Service and Regulatory Announcements (1942) recorded the interception of *P. citricarpa* on oranges from South Africa. In 1945 Wager recorded that the disease was then severe not only in the mist-belt of Pietermaritzburg, Natal, but also in other areas of that State, and stated that it had "spread alarmingly in the last few years and is now causing heavy losses". The disease was recorded for the first time from Town Bush and Chase Valley, Otto's Bluff, Richmond, Bulwer, the Umkomaas Valley (which is very hot and dry thorn veldt with an annual rainfall varying from fourteen to forty-three inches), Verulam, and finally Nkwalini Valley (where an average rainfall of twenty-nine inches is recorded). Wager later (1946) reported the extension of the disease into the Transvaal at Duiwelskloof, Politsi Tzaneen, Nelspruit and Barberton.

The disease so far has not been recorded in any citrus-growing area in the United States.

As far as the writer has been able to determine, this survey covers all of the literature on Black Spot. This paucity is surprising when the severity of the disease under certain circumstances is considered, but reasons will be put forward later for considering that the disease may occur in more citrus-growing countries than this survey would lead one to believe.

ECONOMIC IMPORTANCE.

The importance of this disease in the coastal citrus-growing areas of New South Wales was recognized even when the industry was in its infancy. Benson (1895) records that orange fruits were perfectly clean in the orchard during August and even into September, but the fruit was severely diseased by October, and to the extent of 100% in November. Further evidence of its economic effects is given by Cobb (1897), McAlpine (1899), Allen (1902), Darnell-Smith (1919), Noble and McCleery (1931) and McCleery (1939).

The early observations on the severity of the disease were confined to common orange seedlings and other earlier maturing varieties. With the advent of more extensive plantings of the late hanging Valencia orange, especially after the 1914-18 war, the disease was observed to take on an even more serious form, as mature fruit on such trees was usually allowed to hang in the trees into the summer, and in some districts into the early autumn.

Not only does the disease cause personal loss to the individual citrus grower on the coast, but the suddenness with which the disease usually develops throughout a particular district has a depressing effect on the wholesale market price of this particular type of fruit. When an epiphytotic is at its worst every grower with affected Valencias attempts to market his fruit. Glut conditions develop on the local Sydney fruit market and prices drop rapidly. Instead of orderly marketing proceeding over a period of five months, affected fruit has to be marketed during a short period in October, and the grower, through fear of the disease developing on what clean fruit remain, usually markets these also on a depressed market. Exporters of fruit to other States and to tropical areas handle "clean" Valencia fruits from Black Spot districts with very little confidence during summer months, because of the likelihood of the disease developing in transit from latent infections. In the peak Black Spot seasons between 1929 and 1939 it was not uncommon for clean Valencia fruit to be sold on the wholesale market in October for three shillings and sixpence per bushel case, whereas in February, five months later, clean fruit from the same orchard would, not uncommonly, be sold for twenty-five shillings per bushel case.

The economic effect of the disease is brought out clearly in the Report of the Royal Commission of Inquiry into the Fruit Industry of New South Wales (McCulloch, 1939).

Despite the serious nature of the disease in some localities, other areas on the coast were known where the disease occurred in a very mild form. Individual fruits developed inconspicuous lesions which did not greatly affect their value, while the majority of the fruit was free from the trouble. Orangeville and The Oaks were areas of this type. The disease may not even have been recorded for several seasons in the interval between those occasions when the disease was observed in a very mild form. This experience continues to be substantially true of these districts today.

In the Gosford district, on the other hand, the disease in most seasons is usually serious. This is an area with approximately six thousand acres of citrus orchards with a production of over one million bushels of fruit. Losses in Valencias due to Black Spot, prior to the adoption of control measures, have been placed conservatively at an average figure of between £50,000 and £70,000 per annum. In some years losses might be three times this figure.

SYMPTOMS OF THE DISEASE ON THE FRUIT.

The symptoms of Black Spot on the fruit were first described by Benson (1895). He referred to the manner in which spots rapidly increased in size and grew together, and the rapid appearance of the disease in October on orange fruits which had been perfectly clean and free of disease up till that time. With regard to the time of development of the disease, he stated ". . . the disease does not appear to attack the fruit to any extent till it is thoroughly ripe when it spreads very rapidly . . . rendering it more or less unsaleable, in fact very badly infected fruit falls from the tree and is valueless". He also remarked that the disease developed in the fruit case after packing if left for any length of time. He was of the opinion that the disease spread from diseased to apparently clean fruit, as the development was more serious in cases of fruit where spotted oranges had originally been packed with clean fruit.

Cobb (1897) gave more precise details of the appearance of the disease at that time. ". . . the diseased spots occur as more or less isolated roundish sunken at first, dark coloured spots, the interior portion of which, however, at maturity is lighter

coloured with small dark spots (pustules) at the points where the spores break forth." A similar description is given by McAlpine (1899) with this addition, that the size of the lesions varied from one-eighth of an inch or less up to ". . . irregular confluent brown patches of half an inch or more". These descriptions give an accurate picture of certain phases of the disease development as it is now known.

Several types of lesions can be recognized in the course of the development of Black Spot on Valencia orange fruits. Growers refer to various phases of development as "Hard Spot" or "Shot-hole Spot", "Freckle Spot" and "Spreading" or "Virulent Spot". These different types of lesions are well defined, occurring at various stages, depending on the advance of the season and the maturity of the rind of the fruit.

Hard Spot and Shot-hole Spot.—Valencias are usually fully coloured by the end of May and the disease is rarely seen before mid-August. Where a limited amount of Black Spot development occurs early in the spring on Valencia fruits which are coloured but not yet mature, small lesions several millimetres in diameter result (Plate xv, figs. 1, 2). Such lesions may be very few in number usually, but occasionally fifty or more per fruit may be observed (Plate xv, fig. 3; Plate xvi, fig. 1). They are at first circular and brown with slight depressions. The lesion does not increase very greatly in diameter, but tends to sink in the centre, creating a crater-like depression. The tissue within the crater turns a grey-white colour and pycnidia may develop therein. The rim of the crater-like lesion is usually black and around it is a ring of green rind tissue, contrasting markedly with the normal orange colour of the fruit. No further disease development is usually encountered from those particular lesions, but more active forms of the disease may develop at a later date from the remainder of the apparently healthy rind tissue on such fruit, or on other unaffected fruit hanging in the tree.

In the course of Hard Spot development a limited amount of fungal growth takes place in response to a favourable combination of environmental factors, but some physiological factors associated with the immaturity of the rind cells in some way slow up the rate of growth of the fungus, finally killing it. This has been shown repeatedly by pure culture methods.

Freckle Spot.—Where environmental conditions continue to be favourable, the formation of Hard Spot lesions gradually ceases and the Freckle Spot phase begins. Fruit showing Hard Spot lesions, although disfigured somewhat, has reasonable keeping qualities after being harvested, but where Freckle Spot is present the keeping quality is greatly reduced, and moreover this phase of the disease is only brief, giving way within a week or two usually to an even worse type of lesion.

Freckle Spot (Plate xvi, fig. 2) gets its name from the manner in which a number of small developing lesions appear simultaneously on one-half or portion of the fruit surface, usually that exposed to the sun. As many as fifty to several hundreds of separate, deep orange to brick-red lesions appear together on the surface of the rind within two to four days. The greatest number of lesions of this type counted on a single Valencia fruit was 729. Certain types of fruit may develop only a few lesions but the kind of spot is basically the same.

Many Valencia fruits on trees of similar age in similar situations become affected in this way much about the same time. The lesions are at first about a millimetre in diameter and slightly depressed at the centre. They grow rapidly and usually reach a size of two to three millimetres in diameter before turning brown in colour, and ceasing to make any further noticeable growth. By this stage the depth of the lesion may have increased considerably, depending on the thickness of the rind, and its shape is usually in the form of a hemispherical depression. The important difference between this stage of the disease and "Hard Spot" is that there is no green ring around the lesion, and the causal organism within the morbid tissue is still alive. This latter fact has been demonstrated by pure culture methods. The fact that the causal organism is not dead, and that the lesions are capable of continued slow growth, greatly affects the market value of such fruit. Following periods of hot weather, the growth rate of the fungus in this

type of lesion can suddenly increase and the lesion rapidly enlarge. Apart from its definitely unattractive appearance, infected fruit has a limited life and quick handling by juice factories is the only worthwhile means of disposing of it.

Virulent Spot.—The next phase in the development of this disease on Valencia orange maincrop fruit is the appearance of the Spreading, Confluent or Virulent Spot as the disease is variously known. The latter name is the most common. As the rind of the fruit reaches full maturity, with the onset of warmer conditions, Virulent Spot begins to appear both on unblemished fruit and fruit with other types of lesions (Plate xvii, figs. 1, 2). This is usually two or three weeks after the appearance of Freckle Spot. Fruit which hitherto has been unaffected by the disease develops lesions with a very rapid growth rate, so that two-thirds of the fruit surface may be involved by the activity of a single lesion in four or five days. Where in the earlier phases many separate lesions developed slowly together, now one or at the most several separate infection centres develop into rapidly growing lesions, black in the centre from the multiple development of pycnidia, brown further out due to the necrosis of the rind tissue, and with a narrow brick-red active peripheral area several millimetres wide, forming the margin to the sunken lesion (Plate xv, fig. 4; Plate xvi, fig. 4; Plate xviii, figs. 1 and 2). The lesions at this stage assume irregular shapes. Fruits that had previously developed multiple lesions of Freckle Spot may develop one or several virulent lesions, either from former Freckle Spot lesions that have re-commenced activity, or directly from latent mycelium in the rind tissue (Plate xvi, fig. 3). That the virulent stage of the disease is not brought about by the confluence of all the separate Freckle Spot lesions can be observed in fruit of this nature. The advancing periphery of a single virulent lesion on a fruit may be observed to engulf the former Freckle Spot and Hard Spot lesions, although they can still be recognized within the confines of the much larger virulent lesion (Plate xvi, fig. 4; Plate xviii, figs. 1 and 3). Compared with earlier stages of the disease, the Virulent Spot extends more deeply into the tissue of the albedo, even to the extent of involving the entire thickness of the rind tissue. An epiphytotic of Virulent Spot usually occurs when the Valencia fruit is at peak maturity, and at a time when a temporary abscission layer is forming in the peduncle. Affected fruit falls readily and in orchards where protective spraying has not been adopted, half the crop has been known to drop within several days (Plate xviii, fig. 4). In a year when the disease is severe, many orchards will be similarly affected much about the same time. This fruit has no value, and juice factories are prepared to handle only a fraction of the rapidly deteriorating fruit in the district.

It is clear that as the season progresses and the rind of the fruit approaches maturity, the ability of the mycelium arising from latent infections is progressively more capable of developing satisfactorily in the rind tissues, and so producing more active and serious lesions.

The distribution of the diseased fruit on a tree is of interest. The first fruits to be affected are always on the northern to north-western sector of the tree. These fruits are exposed to warmer conditions and are always earlier in maturing than fruit elsewhere. Ultimately fruit right throughout the tree will become affected, but the type and severity of lesions is always worse in fruit from the northern and north-western sector. Although fruit does appear to be affected earlier, and more severely from this side of the tree, no such difference is noticed with regard to disease gradients in a vertical plane. Fruit from the tops of the trees is just as severely affected as from the lower portions. There is no similarity to the development of Melanose (*Diaporthe citri* Wolf.) which affects fruit usually on the lower portions of the trees. Melanose is spread in the tree by water-borne pycnidiospores (*Phomopsis* stage). The distribution of Black Spot-affected fruit in a tree indicates that the inoculum is air-borne.

No Black Spot develops on the mature fruits of young trees. Valencia trees may bear apparently disease-free fruit up to their seventh, eighth and ninth years. Usually about this stage Black Spot shows up on the fruit though sometimes the trees may be a little younger or the appearance of the disease may be delayed several more years.

Usually, too, when Black Spot develops on fruit for the first time in a particular block of trees, the lesions are mainly of the Hard Spot type and all trees bear some affected fruit. The absence of Black Spot lesions is not due to lack of infection. Latent infection has been demonstrated by pure culture methods to be present in the rind of a fruit from young trees. This is an explanation of the fact that Black Spot appears in an orchard for the first time generally without any apparent disease gradient from a possible focal infection point. The disease becomes established in the orchard years before its symptoms occur on the fruit.

The same phenomena are shown by early maturing oranges. An observation made in July, 1940, in a common orange orchard at Mangrove Mountain, illustrates this point. The trees were forty-three years old, and the fruit had never been observed to be affected with Black Spot. It was usually harvested by early spring. Abundant inoculum of the causal organism was found on the leaf litter beneath all the trees. Cultural studies demonstrated the existence of large numbers of latent infections in the rind tissues. The life cycle of the causal organism was being completed but no signs of the disease, as we know it, were ever observed on the fruit. In this case there is no doubt that the principal reason for the non-appearance of the disease of these fruits was that the variety was early maturing and the crop was removed before the onset of summer. Similar observations have been made in Washington Navel orange orchards, most of whose crop is harvested during the winter.

It is rare for the disease to appear in one part of an orchard only, although under special conditions this has been observed. For example, in January, 1941, a bush fire approached the boundary of an orchard of eight-year old Valencias. The trees were not damaged but Black Spot appeared on fruit in the outside rows four or five days later, although it had not been recorded previously in that orchard. The fruit on the remainder of the trees was unaffected. It is usual with bush fires for a local environment to be created and the temperature may reach 112° to 115°F. in its vicinity.

Symptoms of the Disease on Leaves.

Lesions of Black Spot on citrus leaves on the trees are very rare in the Gosford district. When they do occur, it is usually on lemon leaves (Plate xix, fig. 1), very rarely on green Valencia orange leaves. These lesions vary in size from one-sixteenth to one-eighth of an inch in diameter. They are sunken and are visible from both surfaces of the leaf. Usually the leaves affected are senile. As many as several hundred discrete lesions can develop on a single leaf. Such lesions may develop an occasional pycnidium, but the majority are without fruiting structures of the causal organism. Leaf lesions appear to be more common on Valencia orange at Gayndah in Queensland. Wager (1945) recorded the development of leaf lesions of Black Spot on orange and lemon trees in South Africa and in personal communications he has stated that leaf lesions are extremely common in the Transvaal and Natal.

MORPHOLOGY OF THE CAUSAL ORGANISM.

Occurrence of Pycnidia on Fallen Leaves.

It has been demonstrated (McCleery, 1939; Kiely, 1945) that the protective spraying of young fruits on Valencia orange trees with weak strength Bordeaux Mixture programmes can give satisfactory commercial control of Black Spot on the maturing maincrop fruit twelve months later in the following spring and summer. It is evident that the first infections are established in the early fruit stage shortly after petal-fall in October, and can continue for a period up to five months (McCleery, 1939). These infections are capable of surviving in a latent form in the outer tissues of the flavedo, until the following spring and summer. It was generally accepted that the initiations of these latent infections of the fruit were from pycnidiospores produced in pycnidia, which develop upon the Black Spot lesions of affected Valencia fruits. Considerable evidence was available in support of this view since the time of development of the lesions on the mature fruits coincided with the time of fruit setting of the new season's crop. Furthermore, new lesions continue to develop on the apparently healthy mature

fruit hanging in the trees, during the subsequent three or four months. This period coincides with the period during which the following season's young fruit, which are also hanging in the trees, are susceptible to infection.

If infection is caused by pycnidiospores produced on the maturing fruit, removal of the diseased and disease-labile Valencia fruits from the trees prior to blossoming and the setting of the new season's crop in mid-October, which would greatly reduce the pycnidiospore inoculum available, should result in reduced infection of the young fruits. This possibility was tested in isolated orchards by McCleery (1936) and later by Kiely (1941) but no control of the disease was obtained. Black Spot was equally severe the year following early removal of fruit. Other forms of inoculum were therefore suspected. Dead wood and twigs on the trees were examined extensively with negative results. The bark was not found to harbour any form of the fungus. Finally, examination of the dead leaves beneath the trees revealed the existence of an abundant pycnidial development which proved (on cultural investigation) to be *Phoma citricarpa* McAlp.

Such leaves harbouring the pycnidial development may be found in large numbers beneath Valencia, grapefruit, lemon, mandarin and Washington Navel orange trees. Some idea of the importance of this form of inoculum may be obtained when it is realized that almost every leaf, beneath individual trees, is frequently covered by the development of pycnidia of *P. citricarpa* McAlp. Under ideal conditions for their development, these pycnidia are closely studded over the entire leaf surface. They can occur on either the dorsal or ventral surfaces of the leaf, but are usually thickest on one side only, the side or portion of the leaf exposed to the sun's radiation. The sizes of the pycnidia and pycnidiospores produced on these dead leaves agree with those given by McAlpine in his original description (1899).

Occurrence of Perithecia on Fallen Leaves.

Collections and examinations were made of dead leaves from beneath citrus trees from a large number of localities. On a great number of the older leaves an ascigerous fungus was discovered to be very common (Plate xx, figs. 1, 2). Study of this fungus revealed that it conformed with the description of the genus *Guignardia*. Microscopic evidence indicated that a relationship was most likely between *P. citricarpa* McAlp, and this undescribed ascigerous fungus. Certain difficulties of technique had to be overcome before this connexion between an imperfect fungus and an ascigerous stage could be established. Ultimately eighty-three cultures were obtained from single ascospore isolates. These agreed in all respects with cultures from pycnidial material of *P. citricarpa* McAlp. So far, however, attempts to produce the ascigerous form of the fungus under pure culture conditions have consistently failed. Infection studies on lemon fruits, using ascospore isolates, have, however, proved the pathogenicity of this ascigerous fungus and its aetiological relationship to the Black Spot fungus.

Isolation of the ascospores in pure culture was accomplished by inverting agar plates over moistened portions of dead citrus leaves known to possess ripe asci within the perithecial structures. The high degree of success with this technique indicated that the ascospores were released explosively and that this form of the inoculum was air-borne. The identity of these ascospore cultures with *Phoma citricarpa* McAlp. is of considerable importance, since it means that an abundant source of wind-borne inoculum of the causal fungus exists, constituting the primary means of spread of the disease, as well as an efficient method of carry-over for the fungus.

The Pycnidia on Dead Citrus Leaves.

Three types of pycnidial structures of *P. citricarpa* are encountered on the fallen leaves of citrus under central coast conditions. All are of similar size, but their functions are different. These different structures are the true functional pycnidia, the spermogonia and the pycnidio-sclerotium.

The true functional pycnidium developing in lesions on citrus fruits has been described adequately by McAlpine (1899). The following additional observations,

however, are noteworthy. The pycnidiospore production is continuous, the sporogenous layer being regenerative. The pycnidial cavity, just prior to maturity, is filled with a jelly-like substance. Darnell-Smith (1919) has already commented upon this. He noted ". . . dissolution of the cell walls of the pseudo-parenchyma at certain foci . . .". He also referred to the appendage which can sometimes be seen attached to each pycnidiospore. This, he claimed, was the remains of the sporophore. It is certainly true that many pycnidiospores do possess this appendage, but thin stained sections of developing pycnidia reveal that the pycnidiospores while still attached to the sporophore possess a terminal gelatinous cap, which later shrinks to form the appendage (Text-fig. 1). Its origin is clearly not from the sporophore, but more probably from the histolysis of the thin-walled pseudo-parenchymatous tissue which originally filled the pycnidium.

Subsequent crops of pycnidiospores do not possess this mucilaginous envelope and appendage. If the immature pycnidiospores are removed forcibly from the pycnidium by pressure they are seen to be aggregated together in a gelatinous matrix. This matrix can be demonstrated by overstaining the pycnidiospores with a basic stain such as Gentian Violet or Thionin. When mature spores are allowed to escape naturally from the pycnidium into a drop of water on a slide, they are not aggregated together, but orientate themselves equidistantly throughout the surface plane of the water, as though each spore possessed a similar electric charge. The mucilaginous sheath in overstained preparations is seen to surround the entire pycnidiospore, and at one end the apex is protracted out into a hyaline appendage, sometimes 20μ in length.

Pycnidia have been observed in which the first formed pycnidiospores do not appear to possess this hyaline appendage. The possibility of the existence of two types of pycnidia, a dormant type exhibiting the phenomenon of histolysis of the pseudoparenchyma, and a normal "*Phoma* type" pycnidium without appendage to the pycnidiospores, requires further investigation.

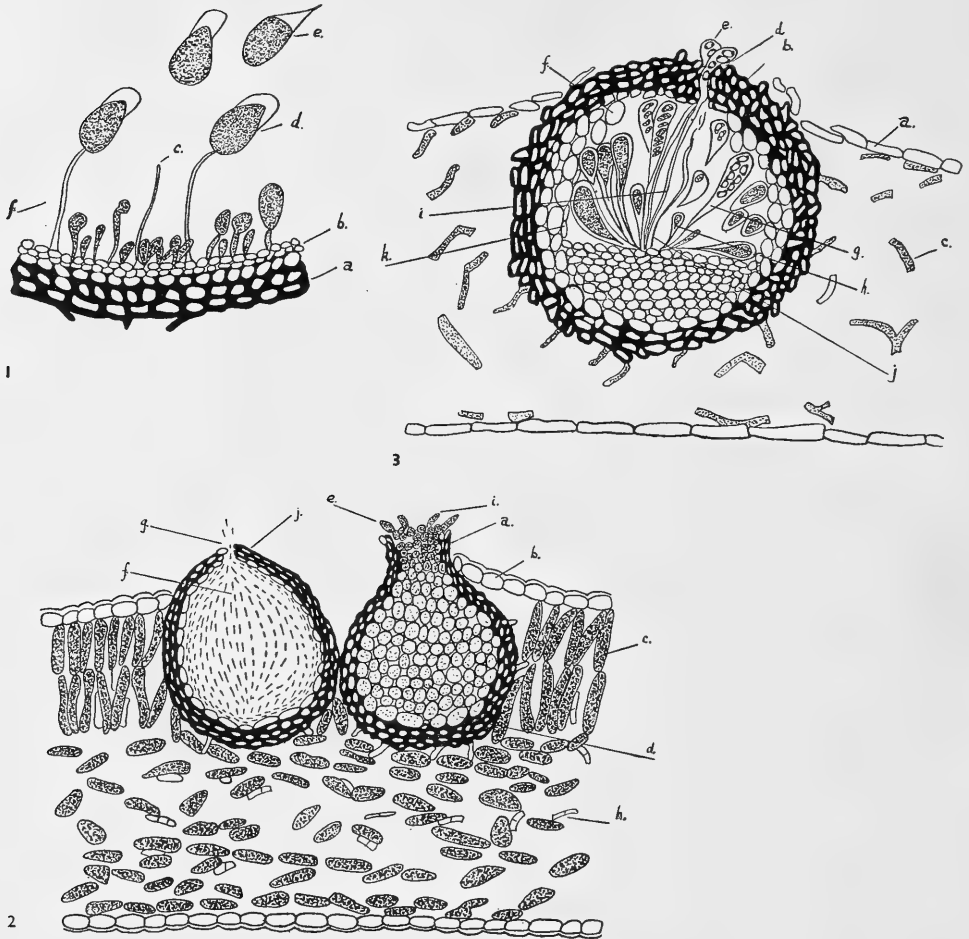
Other investigators have referred to the phenomena of histolysis and the presence of the hyaline appendage to the pycnidiospore. Shear (1905, 1907) mentioned them with regard to the imperfect pycnidial form of *Guignardia vaccinii* Shear. Reddick (1911) referred to the histolysis, but could not see the appendages to the pycnidiospores of *Guignardia bidwellii* (Ellis) Viala et Ravaz, appendages which Shear earlier (1907) had described for this particular parasite. Guba (1925) described similar phenomena in the Apple Blotch organism (*Phyllosticta solitaria* E. & E.). All of these organisms, including the last named, showed many features of similarity to the causal organism of Black Spot of citrus.

The Spermogonium on Dead Citrus Leaves.

The spermogonium produces very great numbers of bodies, described by Darnell-Smith (1919) as "X-spores". He considered they were produced in pycnidia. However, there is strong evidence to regard them as functional male gametes, entitled to be called spermatia. It is extremely rare to find them occurring on fruit lesions, but they are to be found very commonly on recently fallen dead leaf material from orange and lemon trees (Text-fig. 2). Spermogonia also are produced in abundance in pure cultures of *P. citricarpa*. Their appearance always precedes ascocarp formation in dead leaf material and so, quite possibly, they have a distinct sexual function. Similar structures have been described by Reddick (1911) for *G. bidwellii* (Ellis) Viala et Ravaz, by Blackman and Welsford (1912) for *Polystigma rubrum* DC. and by Craigie (1927) for *Puccinia graminis tritici* E. & H.

The Pycnidio-Sclerotia on Dead Citrus Leaves.

The pycnidio-sclerotia occur on the dead leaves of citrus and also in culture upon almost all types of artificial media so far tested. They resemble a functional pycnidium, morphologically, except that their interior is composed of a compact mass of pseudoparenchymatous tissue (Text-fig. 2). Investigations are in progress on the



Text-figures 1-3.

Text-fig. 1.—Section of portion of pycnidium showing (a) pycnidial wall, (b) hymenial layer, (c) remains of sporophore after dehiscence of pycnidiospore, (d) mature pycnidiospore still attached to the sporophore. The adhesive cap to the spore is shown. (e) Ripe pycnidiospore with appendage developing from the jelly-like cap. (f) Immature pycnidiospore arising from the hymenial layer.

Text-fig. 2.—Section of dead Valencia orange leaf, seven days after removal from tree, showing the spermogonium and the pycnidio-sclerotium developing side by side. (a) Pseudo-parenchymatous perithecial wall. (b) Epidermal tissue of leaf, still unaffected by the fungus. (c) Dead and dying cells of the palisade tissue. (d) Large cells of inner pseudo-parenchymatous tissue. (e) Small cells of the inner pseudo-parenchyma, densely cytoplasmic at the apex of the pycnidio-sclerotium. (f) Spermatia within the spermogonium. (g) The ostiole of the spermogonium forming by mechanical rupture of the outer, carbonaceous pseudo-parenchyma. (h) Strands of intercellular fungus.

Text-fig. 3.—An oblique section through a mature perithecium. Section cut through ostiole. (a) Epidermal cells of leaf. (b) Carbonaceous outer pseudo-parenchymatous wall of perithecium, derived from the pycnidio-sclerotium. (c) Mycelial strands completely replaced the host mesophyll tissue. (d) Perithecial ostiole formed by mechanical rupture and histolysis (?) of the outer pseudo-parenchyma. (e) Ripe asci (two) protruding through the ostiole. Ascospores are aggregated at the tips of the asci. (f) Large cells remaining of the original pseudo-parenchymatous tissue of the pycnidio-sclerotium. (g) Ascus with mature ascospores. The base of the ascus is about to elongate and bear the structure up to the ostiolar opening. (h) Immature asci still forming. (i) Elongated portion of ascus which is protruding through the ostiole. (j) Remains of ascus after the ejection of the ascospores.

function of this structure, and evidence will be presented in a later paper that the ascocarp arises within the pseudoparenchyma, the outer wall of the pycnidio-sclerotium becoming the perithecial wall.

The Structure of the Perithecia.

The structure of the perithecium is shown in Text-figure 3. The technical description of this perfect stage of the Black Spot fungus is as follows.

GUIGNARDIA CITRICARPA, n. sp.

Perithecia solitaria, 125–135 μ crassa, vel 2-aggregata 220–240 μ crassa, vel 3-aggregata, 340–360 μ crassa. Stroma nulla. Perithecium globosum ex pycnidio-sclerotio natum, sub-epidermale tandem erumpens, sine rostro manifesto sed denique cum ostiolo 14–16 μ crasso. Peridium 20–22 μ crassum, carbonaceum, luco transmissio fuscum.

Asci in perithecii 45–60, 50–85 μ \times 12–15 μ , ex base perithecii natentes, clavati cylindrici, octospori, ascosporis uniseriatis vel tandem biseriatis. Ascosporae hyalinae vel granulatae griseaeque, plerumque in media tandem guttulo uno magno, non septatae sed raro ad apices uniseptatae, 8.0–17.5 μ \times 3.3–8.0 μ , ad apicem utrumque operculo parvo rotundo hyalino mucilagineo. Paraphyses periphysesque nulla. Fungus citri folia putrida utrumque nec fructus habitat.

Type specimen collected at Gosford, New South Wales, September, 1938.

Perithecia solitary 125–135 μ also in groups of two 220–240 μ and three, 340–360 μ . Perithecial wall 20–22 μ thick. Carbonaceous dark brown by transmitted light, globose, developing from a pycnidio-sclerotium. Sub-epidermal, finally erumpent, no stroma present nor distinct beak, but an ostiole 14–16 μ diameter at maturity. Asci 50–85 μ \times 12–15 μ , 45 to 60 in number arising from the base of perithecium, clavate; cylindrical, eight spored, uni-seried changing to bi-seried at maturity. Ascospores, hyaline to granular grey, usually with one large central guttule at maturity. Non-septate but occasionally with septum near one end of the ascospore, 8.0–17.5 μ \times 3.3–8.0 μ , with a small round clear gelatinous cap at each end. Paraphyses and periphyses absent. Occurring on the ventral and dorsal surface of decaying leaves of citrus, never on the fruits.

The Relationship of P. citricarpa McAlp. to the Genus Phyllostictina Syd.

Sydow (1916) described a new genus, *Phyllostictina* in the Fungi Imperfecti based on the monotype *Phyllostictina Murrayae* Syd. occurring on living leaves of *Murraya koenigii* sent to him from India. His concept was of a pycnidium filled with a pseudoparenchyma whose histolysis gives rise to the pycnidiospores. His description, which was based on a single specimen, stated that sporophores were absent and the pycnidia ceased to function further after the discharge of one spore crop. Later von Höhnel (1920) examined the type specimen of *Phyllostictina Murrayae* Syd., and recognized its close similarity of characters with *Phoma uvicola* B & C, the imperfect spore form of *Guignardia bidwellii* (Ellis) Viala et Ravaz. He stated that in his examination he found no trace of conidiophores although he assumed they had been present and had been dissolved. Von Höhnel assumed that both of these fungi belonged naturally to the same form genus, and to render such a conception tenable he amended Sydow's description of the genus *Phyllostictina* to include species in which the pycnidiospores are borne upon simple, mostly short and evanescent conidiophores. Later Shear (1923) modified the conception of this genus still further, restricting its application to the pycnial forms of the genus *Guignardia* as applied to species congeneric with the common *G. bidwellii*.

The pycnidial form of the Black Spot fungus, namely *Phoma citricarpa* McAlp. exhibits histolysis of the pseudoparenchyma within the pycnidium, conidiophores are present, and its ascigerous form is congeneric with *G. bidwellii*. Hence if Shear's conception is tenable, the imperfect spore form is congeneric with his amended description of *Phyllostictina*. In correspondence with Dr. C. L. Shear concerning the nomenclature of *Phoma citricarpa* McAlp., from descriptions forwarded, and its connection

with *G. citricarpa* n. sp., Shear expressed the opinion that the imperfect spore form of the citrus Black Spot fungus was a *Phyllostictina*. However, the possibility of conflict in the concepts of Sydow, von Hohnel and Shear regarding the genus *Phyllostictina* requires that further investigation be made before deciding whether *P. citricarpa* McAlp. should be included in Shear's amended genus *Phyllostictina*.

HOST PLANTS.

Citrus Fruits.

At the Narara Viticultural Nursery opportunity was afforded to record the susceptibility of a number of varieties of citrus under conditions of natural field infection. The following varieties were observed to be moderately susceptible: Eureka lemon, Lisbon lemon, Chegwyn's lemon, Villa Franca lemon, Thornless lemon; Belair, Genoa Sicily citron CS9; lime seedling; Maltese blood, Golden Nugget, Ruby Blood, Jaffa, Washington Navel, Thompson Navel and Australian Navel orange; Wheeny grapefruit, Djerack nepis, Marsh grapefruit; Emperor mandarin, Thorny mandarin; Siletta orange and kumquat. Valencia orange and common lemon are highly susceptible.

Latent Infection in Other Host Plants.

When it was found that a wind-borne source of inoculum (ascospores) existed in the perithecia that had developed on fallen citrus leaves as well as the water-borne pycnidiospore inoculum produced on the fruit lesions, it was considered likely that elimination of both these forms of inoculum just prior to the opening of the bloom on Valencia trees in a reasonably isolated orchard should give some measure of control of Black Spot. In the spring of 1940 an acre block of Black Spot-labile Valencias was chosen about half a mile distant from the nearest citrus planting. The mature fruit was removed prior to blossoming and the entire ground surface of the orchard was sprayed with a 1% solution of sodium di-nitro-ortho-cresylate, following much the same technique that Keitt (1940) has developed in the use of eradicant sprays for destroying ascospore inoculum of *Venturia inaequalis* (Cke.) Wint. Subsequently it will be shown that under spring conditions about sixteen weeks are required from the time an individual leaf falls until ascospores are ejected. Hence the use of an eradicant spray just prior to the opening of the bloom would ensure that little ascospore inoculum would be liberated for about sixteen weeks, an interval that would cover the greater part of the period of susceptibility of the young developing fruits. Although the action of sodium di-nitro-ortho-cresylate solution successfully eradicated the perithecial material, no success was obtained in controlling Black Spot.

Other sources of wind-borne inoculum were therefore suspected, and an examination was made of many of the native shrubs, vines and trees in bushland surrounding orchards. The following species were found consistently to harbour latent infections of *G. citricarpa* in the leaves: Waratah (*Telopea speciosissima* R.Br.), the wild Sarsaparilla (*Smilax australis* R.Br.), the Turpentine tree (*Syncarpia laurifolia* Ten.), the Christmas Bush (*Ceratopetalum gummiferum* Sm.), and the red flowering Bottlebrush (*Callistemon lanceolatus* DC.) and the Rock Lily (*Dendrobium speciosum* Sm.).

Latent infections have been determined in the foliage of other plants as well, which do not normally occur in the bushland, but frequently are found in local gardens. Among them are Camellias (*Camellia japonica*), Magnolias (*Magnolia* sp.), Holly (*Ilex aquifolium*), the Youngberry (*Rubus* sp.) and the Almond (*Amygdalis communis*).

On some of these plants, especially on the old leaves, restricted lesions up to 2 mm. in diameter sometimes develop. These have been observed on the Waratah, the wild Sarsaparilla, Holly and Rock Lily. In the instance of the Turpentine tree small lesions develop around hypertrophied areas on the green leaves where egg deposition within the leaf tissue due to species of gall-forming Psyllid has taken place (Plate xxi, figs. 2 and 3).

The technique for development of latent infections, which is described later, was originally worked out successfully for citrus leaves, but was found to be equally

successful, with minor modifications, in the development of latent infections on these various alternate host plants.

The pycnidial form has been developed on the dying and dead leaves of most of the plants listed above. With *Smilax* (Plate xx, fig. 3), *Telopea* (Plate xxi, figs. 1, 4 and 5), *Syncarpia* (Plate xxi, figs. 2 and 3) and *Camellia* (Plate xxi, fig. 6) all forms of the fungus (spermatial, ascigerous and pycnidio-sclerotial) have been developed on the dead leaves. Morphologically in the natural state and under controlled conditions in culture these fungi appear to be identical with *G. citricarpa*.

The first case of a species not belonging to the genus *Citrus* which was found to harbour latent infections of *G. citricarpa* was that of almond seedlings raised at Narara Viticultural Nursery, in the Gosford district. Plants were submitted in 1940 for examination at the Biological Branch laboratory for a root rot condition. The plants were kept in a moist chamber for several days, after which time it was noted that numerous pycnidia were developing upon the upper surface of some of the wilted leaves. Examination revealed the close similarity of this pycnidial fungus to the *Phoma citricarpa* McAlp. stage of the Black Spot fungus of citrus. Isolation, cultural investigation and finally successful inoculation into young lemon fruits supported fully this observation. Subsequently the presence of latent infections was demonstrated on the green leaves.

An important paper was published by Baker and Wardlaw (1937) concerning their investigations of latent fungal infections of various tropical fruits at Trinidad. Studies were carried out on naturally infected mangoes, grapefruits, papaws, avocado pears and tomato fruits. Latent mycelium was isolated from large numbers of apparently healthy fruits. One of the most consistently isolated fungi was one referred to as *Glomerella* sp. Mr. S. F. Ashby, of the Imperial Mycological Institute, who examined cultures of this organism, placed the fungus in the genus *Phyllostictina* Syd. with the comment that the fungus was remarkably like *Phoma citricarpa* McAlp., the causal organism of Black Spot of citrus in New South Wales, Australia. He added that since Black Spot of citrus does not occur in Trinidad, the fungus isolated could not be identical with *Phoma citricarpa* McAlp. Recent work, which will be described fully in a later paper, has shown that on Valencia orange fruit in certain seasons infection by *G. citricarpa* takes place and the existence of latent mycelium can be demonstrated by isolation in fruit which at maturity to a large extent does not develop lesions of the Black Spot disease. Such fruit is apparently healthy when fully ripe. As already stated, in the case of Valencia trees up to six or seven years old, it is not usual for them to bear Black Spot-affected fruit, though latent mycelium can be demonstrated.

The possibility should therefore not be overlooked that the species of fungus occurring as a latent infection of grapefruit and other semi-tropical non-citrus fruits in Trinidad may, in fact, be identical with the causal organism of Black Spot on the east coast of Australia. It is possible that under Trinidad conditions environmental factors may be able to prevent disease development. Whatever these conditions are, they are understood only imperfectly at the present time and will be considered in detail in a later paper.

THE PRIMARY INFECTION CYCLE.

The Experimental Production of G. citricarpa on Dying Citrus Leaves.

The occurrence of latent infections of *G. citricarpa* on citrus fruits raised the question of whether latent infections could occur also on young leaves, only becoming apparent after the leaves have died, or whether the development of *G. citricarpa* on dead leaves beneath the tree was initiated by pycnidiospores falling in drops of water from the tree on to the dying leaves beneath. A number of experiments were therefore made to demonstrate the presence of latent infections and to develop the fungus from them.

Green leaves were removed from a late Valencia orange tree and from a sweet rind (Eureka) lemon tree at Narara. Both trees regularly developed Black Spot lesions

on their fruit, and at the time the green leaves were collected abundant dead leaf material harbouring both the pycnidial and ascospore stages was present beneath each tree. The leaves were placed in moist chambers and incubated at 27°C.

Development of *P. citricarpa* was found to be unsatisfactory mainly because of the vigorous growth of *Colletotrichum gloeosporioides* over the surface of the leaves.

Spermogonia of *P. citricarpa* developed only on about half of the leaves in the samples tested and where they did develop as a pure culture their production was scanty and on part of the leaf only, not at all typical of the robust, densely packed developments of pycnidia, spermogonia and pycnidio-sclerotia that occur on fallen citrus leaves under natural conditions in the orchard. Where acervuli of *C. gloeosporioides* occurred on the same leaf as *G. citricarpa*, the former fungus was the dominant one. It was noted that the leaves where no fungal growth had occurred were dry and brittle, as though they had been allowed to dry out too quickly. On the other hand, where *C. gloeosporioides* was the dominant or impure culture on the surface of these dead leaves, their texture was soft and rather moist. Such leaves had dried out more slowly. In the light of this the possibility of incubating leaves at various humidities was considered worth while.

The same type of result was obtained with samples of untreated leaves and samples surface sterilized before incubation, as follows. The leaves were treated with 70% ethyl alcohol for several seconds, then mercuric chloride 1 in 1,000 for ten minutes, and finally rinsed thoroughly in sterilized water before being transferred to sterilized incubation dishes in the 27°C. incubator.

These experiments demonstrated the existence of latent infection in mature leaves, but ideal conditions for the development of the fungus had evidently not been provided.

The Influence of Humidity on G. citricarpa Development on Dead Citrus Leaves.

Humidities ranging from approximately 1% to 90-100% were set up, using the standard technique as set out by Riker (1936) of saturated solutions of various salts in closed containers. As before, lemon leaves were selected at random from the same sweet rind tree. The leaf sample was divided into two equal lots, one half being untreated and the other was treated in 70% ethyl alcohol, 1 in 1,000 mercuric chloride solution and sterilized water as previously described.

No development took place at humidities of 1% and 25%. At 45% humidity spermogonia were initiated but did not develop. At 73% humidity some spermogonia were initiated on the sterilized leaves and some acervuli of *Colletotrichum gloeosporioides* developed on the unsterilized leaves. At 90-100% humidity a heavy growth of *Colletotrichum gloeosporioides* developed but no *G. citricarpa*.

The Influence of Wilting on G. citricarpa Development on Dead Citrus Leaves.

It was evident that the conditions most favourable for pycnidial development had not yet been found. Accordingly, another experiment was set up. It appeared possible that development of spermogonia, pycnidia and pycnidio-sclerotia on the dead citrus leaves was in some way linked with the moisture condition of the fallen leaves during the first few days they were removed from the tree. It appeared from the experiments with varying humidities that if the leaves are allowed to dry out too quickly during the first several days no fungal development of any kind occurs (Plate xx, figs. 6 and 7). Alternatively, if the leaves are allowed to wilt gradually, no development of *G. citricarpa* occurs, but usually a profuse development of acervuli of *C. gloeosporioides* covers the leaves, presumably from latent infections of this fungus. The problem appeared to be one of providing suitable conditions to allow the latent mycelium of *G. citricarpa* to develop without offering *C. gloeosporioides* a similar opportunity (Plate xx, fig. 5).

It was therefore decided to simulate as closely as possible conditions as they occur in the orchard with the daily drying out of the fallen leaves due to the heat of the sun and the deposition of moisture in the evenings occasioned by dews. As in previous experiments, some treatments included surface sterilization of the leaves with

1 in 1,000 mercuric chloride solution as compared with non-surface sterilized leaves. The drying-out effects of the sun in some of the treatments were compared with treatments where the leaves were not exposed to the effects of the sun. The effect of dew was obtained by immersing leaves in water for half an hour after exposure out of doors. It was found that the best method of exposure of green leaves after removal from the tree was to place them without overlapping in a coarse-mesh flat wire gauze bag, so that each leaf obtained much the same exposure. Thirty-two sweet rind lemon leaves were used in each treatment. The treatments were as follows.

- A. Leaves incubated at 27°C. in a moist chamber.
- B. Leaves surface sterilized and incubated as above.
- C. Leaves exposed to sunlight for 12 hours and incubated as above.
- D. Leaves exposed to sunlight for 12 hours, immersed for half an hour in cold water, drained, and incubated as above.
- E. Same as D, but leaves surface sterilized before immersion.
- F. Leaves exposed to sunlight for 12 hours, immersed for half an hour in cold water, drained and incubated as above for three days. Re-exposed to sunlight for 12 hours, re-incubated.
- G. Same as F, but leaves surface sterilized.
- H. Same as F, with an additional immersion of half an hour in cold water after the second exposure.

Spermogonial initials appeared first in leaves given treatment H on the fifth day after picking; 25 out of 32 leaves bore fructification by the seventh day.

On the sixth day spermogonial initials appeared in leaves given treatments A, B, D, E and G.

By the seventh day the number of leaves on which spermogonia were present was as follows: A, 9 out of 32 leaves; B, 14 out of 32; C, 4 out of 32 (rudimentary only); D, 28 out of 32; E, 26 out of 32; F, 24 out of 32; G, 24 out of 32.

The results indicate that a period of wilting prior to incubation at 27°C. markedly increased the percentage of leaves developing *G. citricarpa* from its latent form. Treatments D, E, G and H, which received the wilting treatment, were all superior to treatments A and B, which did not receive the wilting treatment. Further, treatments B, E and G, in which leaves were surface sterilized before incubation, appeared to be in no way different from treatments A, D and H, in which leaves did not receive the surface sterilization treatment. These experiments prove that latent mycelium of *G. citricarpa* must exist within the tissues of the green lemon leaves when they are on the tree, and only when those tissues are weakened by wilting and death is the fungus able to develop vigorously and produce fruiting structures. The fact that no reduction of development of the Black Spot fungus is achieved by surface sterilization indicates that infection occurs while the leaves are still alive on the tree.

Leaves given treatments F, G and H received an additional twelve hours' exposure to out-of-door summer conditions as compared with treatments D and E. The results indicate that no difference exists between these treatments. This is what might be expected, since fallen leaves in the orchard usually receive hot, dry conditions daily in the spring and summer, and yet *G. citricarpa* develops strongly on them. The results obtained in treatment F were not as satisfactory as the figures represent (24 leaves with *G. citricarpa* out of 32). Spermogonia in this treatment were smaller than average and appeared to have been retarded in their development, nor were they as thickly clustered upon the surface of the leaves. Rudimentary spermogonia were observable also beneath the epidermis of the leaves. This retarded development most probably was due to the omission to immerse the leaves in cold water for half an hour after the second exposure for twelve hours to out-of-door conditions. In treatment C, however, where this immersion of the leaves in water was omitted after the first wilting process an even more drastic effect was produced, since the number of leaves that developed spermogonia of *G. citricarpa* was only four. Such growth of the Black Spot fungus that did occur on these leaves was very rudimentary and aborted. It

would thus appear that although a pre-wilting treatment is necessary for the development of *G. citricarpa* from latent mycelium in fallen leaves, moisture must be restored after wilting if a satisfactory result is to be obtained (Plate xx, fig. 7).

The Influence of Leaf Maturity on the Development of G. citricarpa.

The technique which proved successful for the development of latent infections in mature leaves gave anomalous results when applied to less mature leaves. This is shown in the results of the following experiment. Samples of young and old leaves were collected from the northern side of Valencia orange, sweet rind lemon and Marsh grapefruit trees in an orchard at Peats Ridge. The sampling was carried out on 5th January, 1947.

These leaves were wilted in wire baskets exposed to the sun from 7 a.m. to 6 p.m. the day following collection. On the 7th January they were surface sterilized, washed in sterilized water, soaked in sterilized water for half an hour and drained. A sample of these leaves was then incubated at 30°C. On the 15th January the results of the treatments were recorded on the different leaf samples and are set out in Table 1. Seven leaves were selected for incubation from each group.

TABLE 1.
Influence of Leaf Maturity on the Development of G. citricarpa.

Leaf Material.	Appearance of Leaves.	<i>P. citricarpa</i> Developed.	<i>C. gloeosporioides</i> Developed.
Young orange leaves (three months old or younger).	Green to green-brown but pliable after wilting. Retained pliability after incubation.	$\frac{0}{7}$	$\frac{0}{7}$
Old orange leaves (fifteen months old approximately).	Green-brown but slightly brittle after wilting.	$\frac{7}{7}$	$\frac{0}{7}$
Young lemon leaves (three months old or younger).	Green-brown, slightly brittle in places, yet still green in other parts of same leaf, after wilting.	$\frac{7}{7}$	$\frac{7}{7}$
Old lemon leaves (fifteen months old approximately).	Green-brown to pale brown and slightly brittle after wilting.	$\frac{7}{7}$	$\frac{0}{7}$
Young grapefruit leaves (three months old or younger).	Pale green to green-brown after wilting.	$\frac{0}{7}$	$\frac{6}{7}$
Old grapefruit leaves (fifteen months old approximately).	Green-brown to brown after wilting.	$\frac{7}{7}$	$\frac{0}{7}$

From Table 1 it is evident that there is a marked difference between the results obtained with old leaves and young leaves of the three varieties of citrus tested. It would appear that the young leaves are more resistant to desiccation and so, with similar conditions of exposure, do not wilt so readily as the old leaves. This is indicated by the fact that a high proportion of the young lemon and grapefruit leaves developed acervuli of *C. gloeosporioides*. No acervuli were produced, however, on the young orange leaves. These leaves were sterile and possessed a leathery texture after the incubation treatment. No explanation can be offered for the failure of *C. gloeosporioides* to develop on these leaves, as conditions should have been ideal for them to do so, unless, of course, latent infections of this fungus did not exist within them. This is not likely, as the following experiment indicates.

Since the young leaves appeared to be more resistant to wilting than the old leaves, it was decided to carry out another experiment with the residue of the leaves which had already been exposed for twelve hours out of doors on the 7th instant.

These leaves, after exposure, had been surface sterilized, immersed in water for half an hour and drained. They were then stored in an air-dry state in a cupboard at room temperature. Eighteen days after the first twelve-hour exposure a sample of these leaves was taken and given a second twelve hours' exposure in wire baskets. The following day these leaves were again surface sterilized, washed and soaked as before and incubated at 30°C. The results after seven days are given in Table 2.

It will be observed from Table 2 that there has been a very definite improvement with the results obtained with the new season's leaves, after a second wilting, as compared with the results in Table 1 after one wilting only. Both the Black Spot

TABLE 2.

Leaf Material.	Appearance of Leaves.	<i>P. citricarpa</i> Development.	<i>C. gloeosporioides</i> Development.
Young orange	Green-brown to brown slightly pliable after second wilting.	$\frac{3}{7}$	$\frac{7}{7}$
Old orange	Pale brown and slightly brittle after second wilting.	$\frac{7}{7}$	$\frac{0}{7}$
Young lemon	Brown and slightly brittle after second wilting.	$\frac{7}{7}$	$\frac{0}{7}$
Old lemon	Brown to pale brown slightly brittle after second wilting.	$\frac{7}{7}$	$\frac{0}{7}$
Young grapefruit	Green-brown to brown and slightly pliable after second wilting.	$\frac{2}{7}$	$\frac{7}{7}$
Old grapefruit	Brown to pale brown after second wilting.	$\frac{7}{7}$	$\frac{0}{7}$

and the Anthracnose fungi developed on the young leaves where, with the similar material after one wilting period only, neither fungus developed. It is likely that the single wilting treatment was insufficient to bring about the changes necessary within the leaves to enable even *C. gloeosporioides* to develop, still less *G. citricarpa*. After the second wilting treatment eighteen days later *C. gloeosporioides* developed on similar leaves very profusely, and three out of seven leaves developed *P. citricarpa*. Apparently the second wilting was not sufficient to bring about the changes in the young leaves necessary to prevent the development of *C. gloeosporioides*. Examination of Table 2 will indicate that on all young leaves this fungus developed very successfully. The second wilting did, however, bring about sufficient changes to allow the latent mycelium of *P. citricarpa* to develop to some extent.

A fact which has been considered to be of outstanding interest in this experiment has been the discovery that leaves could be kept in an air-dried condition for eighteen days after the first wilting and immersion in water, be subjected to another exposure to direct sunlight for twelve hours after this period, and still be able to develop both *G. citricarpa* and *C. gloeosporioides*. In fact the ability of the Black Spot fungus to develop from latent mycelium in old leaves was in no way impaired by this treatment, while in the case of the young leaves it was improved.

This indicates that even under very hot environmental conditions, where it might be expected that old fallen leaves would be desiccated too rapidly, resulting in the death of the latent mycelium of *G. citricarpa*, there would be a very high probability that *G. citricarpa* could develop in any new season's leaves that had fallen at this period also. A natural leaf drop is, however, more likely to include leaves in their second and third season of maturity, rather than leaves that might be only three or four months old.

The results of these and other experiments show that fructifications of *G. citricarpa* develop from latent mycelium with somewhat greater ease on lemon leaves, whether young or mature, than on leaves of other varieties of citrus.

Conditions Necessary for Maturation of Ascocarps.

In order to determine what conditions are necessary for perithecia formation and ascospore maturation, an experiment was set up in which the following treatments were tested in November, 1941:

- A. Leaves were removed from a sweet rind lemon tree and placed beneath the tree in a flat gauze container for several months.
- B. Leaves were removed from the same sweet rind lemon tree, wilted out of doors for twelve hours, immersed in cold water for half an hour, drained and incubated at 27–30°C. Every day the leaves were removed from the incubator and placed in cold water for half an hour, after which they were returned to the incubator.
- C. Leaves were removed from the tree and treated as in B, but with this difference: the leaves were removed from the incubator in the late afternoon, immersed in water for half an hour, removed and the excess water allowed to drain, but were not returned to the incubator until the following morning. Leaves treated in this way then received a daily alternation of temperature as well as a daily wetting and drying process.
- D. Leaves were removed from the tree, wilted out of doors for twelve hours, immersed in cold water for half an hour, drained and incubated at 27–30°C, except for weekly examinations, when they were removed from the incubator.
- E. Leaves removed from the tree and treated as in A except that the gauze bag was immersed in water for half an hour each morning.

Leaves were examined by means of the microscope each week for signs of the development of asci and ascospores. Immature asci were detected first in treatments C and E ten weeks after the experiment was commenced, while in treatment A the first immature asci were not seen until the twelfth week, and in treatment B not until the fourteenth week. Although spermogonia, pycnidia and pycnidio-sclerotia were developed on the leaves treated according to treatment D, no immature or mature asci were ever detected. Ripe ascospores were observed after fifteen weeks in treatments C and E, after seventeen weeks in treatment A, and eighteen weeks in treatment B. Ascospores were judged to be ripe when the asci protruded through the perithecial ostiole and liberated the spores when a piece of fertile material was placed in a drop of water. It was found that this stage coincided fairly closely with ability of the perithecia to release ascospores explosively when the leaves were moistened. Ascospores were found to be still maturing and being released explosively from some of these leaves five months after being removed from the tree. By this time the dead leaves were in a very advanced state of decomposition.

The results of this experiment indicate that periodic wetting and drying of leaves and daily alternation of temperatures provide the optimum conditions for ascospore formation (treatments C and E). Where alternations of temperature were not provided, ascospore maturation was delayed (treatment B). In treatment E ascospores matured two weeks earlier than in treatment A. Apparently the daily immersion in water for half an hour, to which the leaves in treatment E were subjected, in addition to the nightly effects of dew and periodic rains, provided more suitable conditions than dew and rain alone.

Conditions in the Orchard as they Affect Production of Inoculum.

It is now possible to appreciate what conditions must be fulfilled in the orchard environment in order that an abundance of mature ascospore inoculum be available.

Leaves that fall during wet weather are most likely to be overgrown with acervuli of *Colletotrichum gloeosporioides*, developing from latent infections. In actual orchard experience leaves that fall from the trees during wet spells are frequently subjected to a wet bacterial breakdown. This form of breakdown can, during prolonged wet spells, result in disintegration of dead leaves that are harbouring partially matured ascocarps and so destroy the developing inoculum. Even leaves that have fallen and have been subjected to ideal conditions for initial development of spermogonia, pycnidia and pycnidio-sclerotia during the first week or so can, where nights without dews are experienced for several weeks, fail to mature ascospores. At best ascospore maturation may be greatly delayed. Such conditions are rare in the Gosford district during the spring, summer and autumn, but in late winter, when westerly winds are experienced, a succession of nights without dew can occur.

On the other hand, leaves that fall during moderately hot weather, and so receive an initial wilting followed by an evening dew, are, should such conditions continue, most liable to develop fruiting structures and finally mature ascospores of *G. citricarpa*. During the spring and summer evening dews are very heavy in the Gosford district, so much so that in the early morning citrus leaf litter beneath the trees is thoroughly saturated. It is considered that the experimental daily immersion of the leaves in water for half an hour would be similar in its effects to these nightly dews. It therefore seems most likely that rain is not essential for the development and maturation of ascospores, although its incidence may hasten the period of ripening (compare treatments A and E).

Very hot weather is not favourable for the early developmental stages of *G. citricarpa* on leaves that fall at such a period. Too rapid dehydration of the fallen leaves is likely to occur during the first day, resulting in the leaves becoming very brittle and pale biscuit-brown in colour. Rapid drying out of the leaves under such conditions apparently results in death to the latent mycelium within the leaf tissue, as leaves exposed under such conditions usually fail to develop pycnidia or spermogonia. Where some development does occur it is sparse and non-fertile. It is possible, however, that even where extremely hot conditions are experienced, and where the saturation deficit is very high, some growth from latent mycelium could occur, provided that reasonably heavy nightly dews were experienced at that time. It may be accepted, therefore, that *G. citricarpa* can develop even in temporary dry periods on leaves which fall from older trees, which provide a sheltered canopy for the leaf litter, and may even mature ascospores. However, all such possibilities depend on the regular occurrence of evening dews to moisten thoroughly such leaves that do fall.

As the result of extensive observations on the development of *G. citricarpa* in leaf litter, it can be stated that mature ascospores are present within the perithecia during the greater part of the year. The maturation of these wind-borne spores does not appear to be restricted to any particular season or part of a season.

The Influence of Tree Age on the Development of G. citricarpa on Dead Leaves.

The following observations illustrate the effect of the local environment on the survival of the fungus in fallen leaves.

In the summer of 1941 (February) a block of four-year-old grapefruit trees was found in the Mangrove Mountain district of Gosford whose leaf litter was devoid of any evidence of *G. citricarpa*. It was known that fruit from these trees had never developed Black Spot in previous seasons, although fruit infections may quite possibly have occurred. Later surveys revealed that many young trees in the district during that period had few if any dead leaves beneath them with developments of the Black Spot fungus. The leaf litter under older trees in other plantings, on the other hand, showed the presence of reasonably abundant inoculum. It was thought that tree age may influence the ease with which Black Spot inoculum may be produced on dead leaves from latent mycelium. Samples of leaves were removed from representative young grapefruit trees and treated for the development of latent infections. Of thirty leaves treated, twenty-eight developed a profuse growth of spermogonia over their

entire leaf surface, while the remaining two leaves developed these bodies over only part of the leaf. This was an interesting instance of trees that produced fruit which did not become affected at maturity with Black Spot and whose leaf litter, at the time of observation, did not harbour *G. citricarpa* but in whose green leaves *G. citricarpa* was present as latent mycelium. Later in the autumn (April) *G. citricarpa* developed on a large percentage of the leaf litter around these trees. The explanation of this phenomenon, most probably, is that the shelter afforded by these young grapefruit trees was insufficient during the late spring and summer to prevent too rapid drying out of the fallen leaves, and consequently the death of the latent mycelium.

The Influence of Bordeaux Sprays on G. citricarpa Development.

In view of the very general development of latent infections in living citrus leaves it was of considerable importance to find out whether they also were present in leaves of trees which had been sprayed with Bordeaux Mixture. Accordingly in 1942 a block of 26-year-old Valencia orange trees was chosen at Erina (Gosford district) which had been sprayed each season since 1936 with the Bordeaux Mixture programme recommended for the commercial control of Black Spot. An examination of the litter beneath these trees revealed that the three types of fruiting bodies of *G. citricarpa* were present on about 90% of the leaves. Green leaves were removed from some of the trees in this block in March, 1942, after the Bordeaux spraying programme (three sprays of Bordeaux Mixture of 2-2-80 strength) had been concluded for the 1941-42 season. Fresh Bordeaux Mixture deposit was present on these leaves from the last spray application (mid-February). The green leaves were surface sterilized and treated in a manner similar to that in other experiments for the development of the Black Spot fungus on the dying leaves. After eight days' incubation at 30°C. spermogonia of *G. citricarpa* appeared on a high proportion of the leaves. This demonstrated that the presence of surface deposits of Bordeaux Mixture on the green leaves in no way interfered with the production of fructifications of *G. citricarpa*, whether they were removed from the tree or fell under natural conditions in the orchard. These conclusions have been confirmed by observations in other Valencia orchards where routine spraying is carried out.

Under orchard conditions in the Gosford district foliage bud movement commences generally in the first or second week of September, and this spring growth is completed in most seasons by the first week in October. As the first spray application for Black Spot control on the fruit is not made generally until the time when petals are falling from the blossoms in the last week of October, there is a period from the first week in September until the last week of October, during which infection of the developing leaves by means of ascospores can occur. Infection studies with ascospores which are described later have shown that under controlled conditions in the glasshouse Valencia orange leaves are susceptible to infection from the time they are half an inch long until about five weeks after unfolding from the growing point.

It is to be expected, therefore, that regular annual applications of three sprays to the fruit would not result in any decrease in the development of Black Spot nor make it possible finally to dispense with protective spraying altogether. This is illustrated by the following experiments. From time to time an orange grower of Erina agreed to leave some Late Valencia orange trees unsprayed, in the middle of an eight-acre block. These trees had been sprayed regularly with Bordeaux Mixture since 1936. Although satisfactory disease control has been obtained, no reduction in the amount of inoculum occurred over the years. In the spring of 1946, the last year of test, a number of trees in this block were again left unsprayed so that the developing young fruit was exposed to whatever wind-borne inoculum might be present in the orchard. The fruits on these trees at maturity in the following spring and summer of 1947/48, were showing a very severe development of Black Spot which commenced to appear during the first week in November, 1947. At this time the trees which had received the routine Bordeaux spraying for this disease during the previous season were quite free of the disease.

This sprayed fruit was allowed to remain on the trees until the first week in February, when the bulk of the fruit was harvested with less than 5% wastage due to Black Spot development over the picking season.

The trial referred to indicated that even after ten years there was no possibility of eliminating the need for spraying with Bordeaux Mixture, or even of reducing the number of sprays. In this regard Black Spot differs from Scab disease (*Elsinoe fawcettii* Jenkins) and Melanose (*Diaporthe citri* Wolf.), both of which are rendered easier to control after a few years of spraying.

Experiments with Foliage Protective Sprays.

The possible value of a spray or sprays applied for the specific purpose of protecting the foliage was next explored. An experiment was conducted at Kulnura (Gosford district) in the spring of 1946. Elongation of the foliage buds on the trees in question commenced on the 3rd September. Three treatments were compared.

- A. Bordeaux Mixture 2-2-80 applied on 5th September.
- B. Bordeaux Mixture 2-2-80 applied on 5th September and again on the 22nd September.
- C. Unsprayed trees.

On 25th October, several days before these trees were due to be sprayed with Bordeaux Mixture 2-2-80 again for protection of the young fruits, samples of leaves were removed from the trees in each treatment. These leaves were surface sterilized and subjected to the standard treatment for development of *G. citricarpa* from latent mycelium. Ten leaves were removed from five trees representative of each treatment, making a hundred and fifty leaves in all, for examination. The following results were obtained:

TABLE 3.

Treatment	A	B	C
Leaves collected	50	50	50
Number of leaves on which <i>G. citricarpa</i> developed	45	48	41

Obviously there is no difference between these, and no limitation of leaf infection with resulting reduction of inoculum carry-over from year to year, even where two Bordeaux sprays have been applied. The amount of protection that could be afforded the rapidly developing leaves was insufficient to prevent infection.

The number of spray applications made for the control of Black Spot on the fruit had to be kept as few as possible since many citrus trees under central coast conditions are liable to show adverse effects due to a slow copper poisoning following upon the use of strong Bordeaux sprays. Hence an increase in the total number of spray applications by one or two additional foliage sprays in September would have to be highly efficient to be justified. It is most likely that three or four foliage sprays in September and early October would give some degree of protection to the young developing leaves; however, this would mean that seven or eight spray applications would have to be made in all, each season to protect the fruit and spring-formed leaves. Such a procedure would not be economic or desirable, from the point of view of tree health.

There are other periods of the year when Valencia orange trees make new foliage growth, however. In addition to the spring growth, under normal conditions healthy trees will develop foliage growth to some extent in January and to a much greater extent in April. In the case of young trees, or of older trees under very favourable autumn conditions, foliage and shoot growth may be made throughout the entire late summer and autumn period. Since ripe perithecia and viable ascospores are available right throughout the entire year, such growth is liable to infection and to sustain latent

mycelium. Therefore, even though a spray programme applied in the spring might protect spring-formed foliage, extensive leaf infections can occur quite possibly in the late summer and autumn. No further investigations along these lines were therefore made.

A comparison can be drawn here with Valencia orange trees that have been sprayed with Bordeaux Mixture in the spring and summer in order to protect the spring setting of fruit (i.e., the maincrop) and which have also set an intermediate crop of fruit from a bloom that occurred in the late summer. If the spraying had been efficient, the main-crop fruit at maturity the following spring and summer will be found to be reasonably free of the disease. On the other hand, the intermediate crop of fruit on the same trees, which will ripen during the period of January to March, has frequently been found to be infected with Black Spot, indicating that wind-borne inoculum was available in sufficient quantity during the period the intermediate crop of fruit was set in March of the previous season.

The Nature of Ascospore Liberation.

Like the ascigerous forms of many other fungi, the ascospores of *G. citricarpa* are liberated with explosive violence when dead citrus leaf material harbouring the mature ascospores is moistened with water. The maturity of the ascospores can be determined fairly accurately by placing dead leaf material of Valencia orange or lemon leaves on which immature, partially mature or mature asci are present in water on a microscope slide for half an hour. If the perithecia are mature, several ripe asci will protrude partially from the ostiole; with gentle pressure on the cover-slip, the extrusion of the asci in a clustered fan-like structure from the perithecial ostiole will result. With immature material the perithecium must be crushed to reveal the presence of the developing asci within.

The technique developed to demonstrate the air-borne nature of the liberated ascospores is as follows. Suitable dead-leaf material was soaked in tap water for thirty minutes. A piece of tissue five millimetres square was cut from the leaf and affixed to the inner surface of a sterilized petri dish lid. This can be accomplished readily by using a drop of sterilized nutrient or washed agar as an adhesive. The piece of tissue is placed with the fructifications on the exposed surface. Within fifteen to thirty minutes, ripe ascospores will be discharged on to the lower surface of the petri dish. Use has been made of this technique in securing pure single ascospore cultures of *G. citricarpa* and ascospores for germination studies. For securing pure cultures, nutrient agar was placed in the lower petri dish, and the fertile material was affixed to the upper petri dish, about an inch from the edge. The dishes were placed on the laboratory bench with the dish lid uppermost, every thirty seconds the upper dish was rotated about 45 degrees in relation to the lower dish containing the nutrient agar. This was continued for fifteen minutes, or until ascospores were being ejected on to the surface of the nutrient agar beneath. This could be verified by examining the plate beneath the two-thirds of an inch objective of the microscope. When the ascospores were thinly sown over the surface of the agar, their position was marked and they were then transferred to nutrient slopes. In this way eighty-three single ascospore cultures were obtained.

The vertical distance which the ripe ascospores can be thrown has been determined as follows. Suitable dead-leaf material bearing mature ascospores was soaked in water for thirty minutes and pieces of tissue 5 mm. square were cut from this material and placed in a central position with the fertile perithecia uppermost, on the upper lens surface of the abbé condenser of the microscope. A microscope slide was then placed in position on the microscope stage about one millimetre above the perithecia-bearing material. As soon as ascospores commenced to be ejected, and were caught on the lower surface of the microscope slide, the abbé condenser was lowered, bearing the ripe perithecial material with it. In this manner, the maximum distance of throw was determined. The greatest distance of vertical throw observed has been of

the order of one centimetre. However, the distance to which a particular ascospore was ejected was found to depend on the time from when ejection first commenced in the particular perithecium. The vertical throw decreased as the time interval increased. Towards the end of the ejection period, which may last two hours, the ascospores were ejected and thrown a vertical distance of one or two millimetres only.

An efficient method of wind-borne dispersal of inoculum of *G. citricarpa* has thus been demonstrated. When it is considered that every green leaf on every citrus tree in a district where there are seven thousand acres of trees, is capable of developing and maturing ascospores, the enormous potential of wind-borne inoculum with this disease is realized.

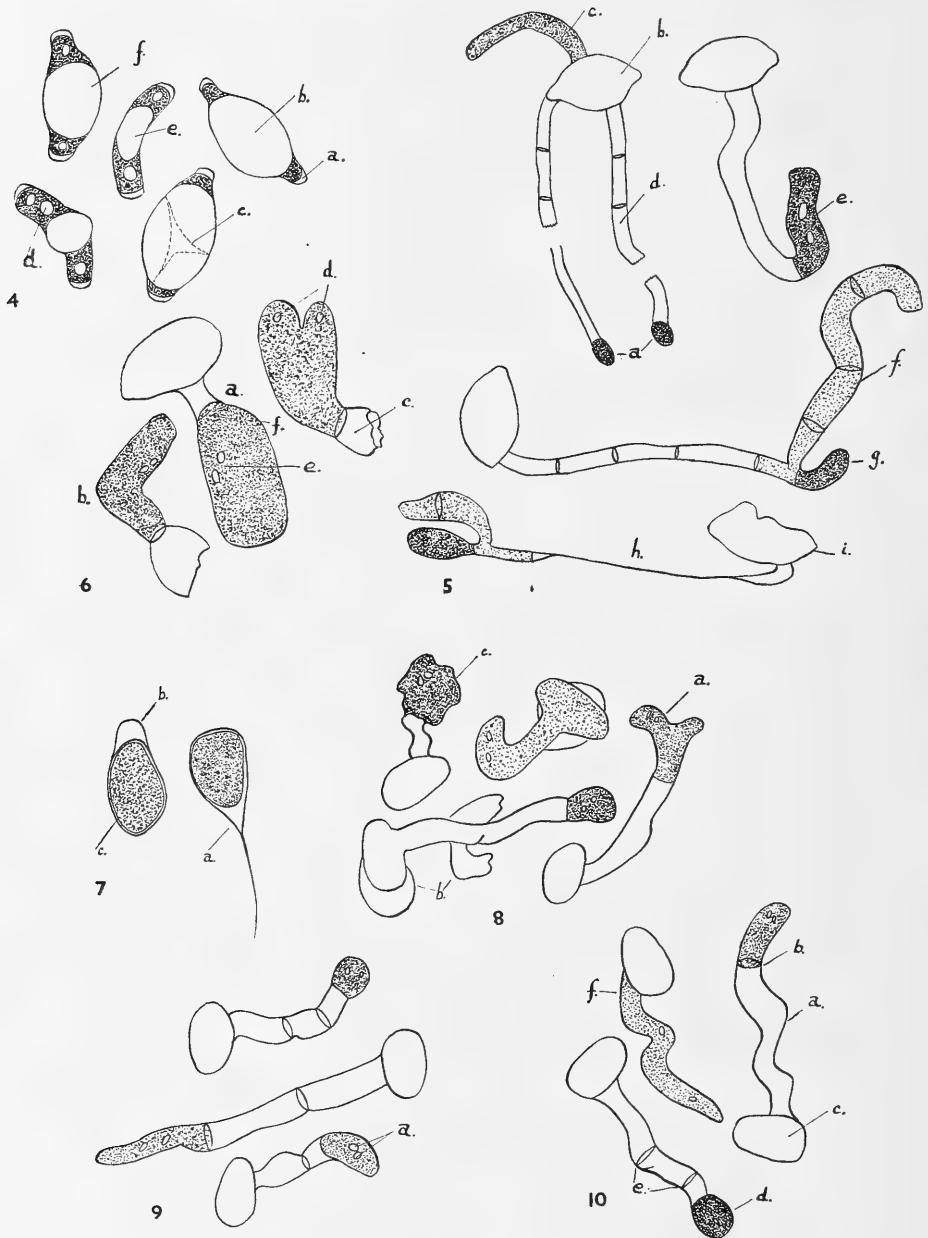
Germination of Ascospores.

Germination studies were carried out with ejected ascospores which had matured under natural conditions in the orchard. In Table 4 percentages of germination of ascospores on the surface of potato dextrose agar are given. Ascospore germination trials were carried out at 25°C. in triplicate. The test was commenced within fifteen minutes of ascospore ejection.

TABLE 4.

Time.	Replicates.	Percentage Germination.	Mean Percentage Germination.
After 8 hours	1	0·0	—
	2	0·0	
	3	0·0	
After 16 hours	1	0·0	—
	2	0·0	
	3	0·0	
After 24 hours	1	0·0	—
	2	0·0	
	3	0·0	
After 36 hours	1	25·2	31·6 ± 6·1
	2	28·3	
	3	41·3	
After 48 hours	1	71·3	70·0 ± 2·7
	2	72·8	
	3	65·9	
After 72 hours	1	80·9	84·5 ± 3·5
	2	89·1	
	3	83·5	
After 96 hours	1	100·0	98·6 ± 3·3
	2	100·0	
	3	96·0	
After 120 hours	1	<i>G. citricarpa</i> colonies commencing to appear on the surface of the agar.	
	2		
	3		

The germination of ascospores (Text-figs. 4-6) was by means of a single germ tube which was contorted and twisted in its growth. By the time the germ tube had grown to a length of 45 μ the entire contents of the ascospore had moved into it. The appearance of the germinating ascospore and germ tube was very similar to that of the germinating pycnidiospore (*Phoma citricarpa* McAlp.); however, two and sometimes three germ tubes were observed developing from a single ascospore, whereas more than a single germ tube has never been observed in the instance of the germinating pycnidio-



Text-figures 4-10.

Text-figures 4-6. Germination of ascospores.

Fig. 4. (a) Adhesive cap to ascospores. (b) Large central vacuole; spores over-stained with Gentian Violet to show the caps to the spores. (c) Cytoplasmic strands across vacuole. (d) Smaller vacuoles which have not developed. (e) and (f) Stages in the enlargement of the vacuole in immature ascospores. Fig. 5. Ascospores germinating on the surface of potato-dextrose-agar. (a) Terminal appressorial body. (b) Empty ascospore with three germ tubes. (c) Germ tube filled with cytoplasmic contents. (d) Germ tube with cross walls, formed as the contents of the germ tube migrated to the growing point. (e) Large appressorium formed on short germ tube. (f) Initiation of mycelium on the surface of agar. (g) Sausage-shaped resting-body. (h) Evacuated germ tube. Fig. 6. Ascospores germinating on surface of glass slide. (a) Short germ tube. (b) Resting body formed directly from germinating ascospore. (c) Remains of ascospore. (d) and (e) Paired nuclei with the resting bodies.

spore. After about forty-eight hours a dark brown terminal secondary spore, which had the appearance of an appressorium, was produced by the ascospore germ tube. At this stage the entire contents of the germ tube, as well as that of the ascospore, had moved into the appressorium, and a septum was laid down between it and the germ tube. The walls of the germ tubes tended to collapse following upon this withdrawal of their protoplasmic contents, and the structure of the cell walls of former ascospores and of the germ tubes became barely discernible. The size of these appressoria varied considerably. It was noted that where the germ tube was short the terminal appressorium was large, and, as might be expected, where the germ tube was long the appressorium was much smaller. The appressoria produced terminally on germ tubes whose length was of the order of 20μ were about $14-16\mu$ in length, or approximately the size of the original ascospore. The smallest appressoria observed were 3.8μ long. These bodies were almost spherical and were produced terminally on each of three germ tubes from a single ascospore, the average length of the germ tubes being 78μ . The largest appressoria were recorded not on potato dextrose agar but where spores were sown directly on the glass petri dish plates moistened with tap water. Here the germ tubes were very short and, in some cases, almost non-existent, the protoplasmic contents of the ascospore moving directly by the germination pore into the developing appressorium which developed an olivaceous brown colour. These bodies measured from 16μ to 20μ and were actually larger than the ascospore from which they had originated. The bodies varied considerably in shape, much more so than where germination had proceeded on nutrient agar surfaces. Some appressoria were sausage-shaped, others spherical, bladder-shaped and pyriform, while still others were shaped like a boxing glove. Kohl (1932) has already commented upon the latter-shaped appressorial body in *Phyllosticta solitaria* E. & E.

In the case of spores germinating on agar where germ tubes had penetrated deeply into the agar, the terminally produced appressoria remained dormant, and no further growth was made. On the other hand, where the germ tube had remained on the surface of the agar, the appressoria germinated within a few hours of their formation. Appressoria which were only 20μ beneath the surface of the agar were delayed up to thirty hours in germinating. Apparently the supply of oxygen plays an important part in the germinating of these appressoria. The mycelium which developed from the appressoria was stouter than the germ tube, averaging 4.5μ in diameter. It was this mycelium which developed and produced typical colonies of *G. citricarpa* after 120 hours.

Appressoria have been noted by many workers. Frank (1883) has recorded them on *Fusicladium tremulae* Fr. De Bary (1886) recorded them in *Sclerotinia*, Aderhold (1896) in *Venturia inaequalis* and Brown (1915) on *Botrytis cinerea* Pers. With fungi more closely related to *G. citricarpa*, Reddick (1911) has recorded their formation on the germ tubes from germinating ascospores and pycnidiospores of *G. bidwellii* (Ellis) Viala et Ravaz, and more recently Kohl (1932) has recorded appressoria on the germinating pycnidiospores of *Phyllosticta solitaria* E. & E. The latter fungus is claimed by Shear (1923) to be a typical *Phyllostictina*, agreeing in every essential respect morphologically with *P. bidwellii*, the pycnidial form of *G. bidwellii*.

The structures observed developing on the germ tubes of germinating ascospores of *G. citricarpa*, and, as will be described later, on the germ tubes of germinating pycnidiospores as well, have been called appressoria, although to date their function in this

Text-figures 7-10. Germination of pycnidiospores.

Fig. 7. Ripe pycnidiospores showing (a) hyaline appendage formed from (b) the jelly-like cap. (c) Guttulate nature of cytoplasm. Fig. 8. Pycnidiospores germinating in 0.5% citric acid. (a) and (c) Mis-shaped resting-bodies. (b) Remains of jelly sheath to pycnidiospores and germ tube, seen only in heavily stained preparations. Fig. 9. Pycnidiospores germinating in 0.1% citric acid. (a) Contorted growth of germ tube. (b) Septum formation, walling off the contents of the germ-tube to form an appressorial-resting body. (c) Empty ascospore. (d) Terminally produced resting body. (e) Septa formed in the germ tube. (f) Normal growth of germ tube in the weaker citric acid solution. Fig. 10. Pycnidiospore germination in presence of orange rind tissue. (a) Paired nuclei in resting body.

respect has not been observed. They may serve also as secondary spores, thus affording the fungus a mechanism of protection when germination has proceeded on the surface of leaf or fruit, and unfavourable conditions intervene. The ability of these structures to act as secondary spores and eventually to germinate, supports this view.

Examination of Table 4 will reveal that after twenty-four hours no ascospores had germinated, and after thirty-six hours less than one-third of the ascospores had germinated. Forty-eight hours after the trial had commenced 70% had germinated. It was not until four days had elapsed that the very satisfactory germination of 98% was recorded. The suitability for germination trials of ascospores collected directly after ejection from the perithecia is well illustrated by such a germination. In the orchard conditions which favour ascospore discharge would also favour ascospore germination after they had lodged on the surfaces of leaves and fruits. Hence a high degree of successful germination should be expected under orchard conditions. This would depend, to a great degree, on the environmental conditions which followed shortly after ascospore discharge in the orchard. If heavy evening dews are experienced on successive nights, favourable environmental conditions would be provided for ascospore germination, and a high percentage of spores could be expected to have germinated four days after ejection. On the other hand, if ascospore discharge occurred after an isolated shower of rain or after a single evening dew, without in either case a succession of dews on subsequent evenings, the probability of germination occurring would be greatly reduced. Further investigation of this point will be carried out.

In respect to ascospore germination of the Black Rot fungus of the grape Reddick (1911) has stated: ". . . the spores germinate slowly even under the most favourable conditions . . . the writer has never succeeded in obtaining germ tubes on ascospores in less than thirty-six hours. It is more often forty or even sixty hours." Reddick also stresses the importance of rains followed by dews, fogs and cloudy days in securing infection with these ascospores. He states, however, that rain is necessary for ascospore discharge. He bases this statement on the observation that new infections on grape berries are related to periods following rain and dews.

Infection Studies with Ascospores.

The first attempts to infect Valencia orange and lemon fruits with the causal fungus of Black Spot were carried out with pycnidiospore inoculum. Those experiments will be discussed later when dealing with the secondary infection cycle.

Infection studies carried out under central coastal conditions were complicated by the fact that wind-borne inoculum was extremely abundant in most orchards, and unless some steps were taken to protect fruit from such inoculum, under these conditions, the results of artificial inoculation would be unreliable. A further complication was occasioned by the fact that the mature fruit of young Valencia trees do not develop lesions even though infection may have been successful on such fruits during the susceptible period as measured by the development of latent infection. Hence to satisfy Koch's postulates, it was necessary to use fruit produced on Valencia trees of a greater maturity than ten years at least, so that it would be reasonably certain that a proportion of the successful infections of the young fruits would ultimately develop as lesions on the mature fruits. Even if infection experiments were conducted in areas where this disease at present does not occur, the possibility of natural infection of the young fruit occurring and the non-expression of the disease on the mature fruit would still exist. Were the pathogen entirely absent from such areas, its introduction merely for infection studies could not be sanctioned. This restricted studies to young fruits on old Valencia trees that had been bagged to protect them from natural infection. In such studies glazine bags were used to protect the blossom and the young fruits from chance natural infection both before and after inoculation. Experiments were tried in 1938, 1939 and 1940 with pycnidiospore inoculum, but a satisfactory technique was not easy to develop. The blossom had to be covered before the flowers opened to eliminate the possibility of natural infection at

that stage. Only a few blossoms usually survived the artificial conditions within the bags. Of those fruits which were set, few remained on the trees so long as bagging conditions were maintained. The small percentage of fruit which survived usually became severely infested with mealybugs, aphids, scale insects and rust mites, so that it became virtually impossible to produce typical mature Valencia fruit infected only with Black Spot. The results of such experiments will be detailed under infection studies with pycnidiospore inoculum.

Inoculation experiments were conducted at the Biological Branch glasshouse, Botanic Gardens, Sydney, during September and October, 1938, using potted citrus trees on trifoliata root stock. These trees usually carried four to six fruits to maturity and could be placed in the glasshouse in incubation chambers. Since ascospore inoculum had not been produced in artificial pure culture, citrus leaf material harbouring mature ascospores was collected at Erina (Gosford district) and used as a source of this kind of inoculum.

The following varieties were inoculated: Valencia orange, Washington Navel orange, Sweet Rind lemon and kumquat. The method of inoculation was as follows. Dead lemon leaves harbouring the ripe ascospore inoculum were soaked in water for fifteen minutes, drained and loosely wrapped around the very small fruits on the potted trees. Such fruits were atomized with water before and after the dead leaves were placed around them. Moist cotton wool was then loosely wrapped around the fruits to hold the leaves in position. Each tree was then placed in a large sheet metal incubation can with a glass top. This incubation can was thoroughly atomized with water to maintain saturated atmospheric conditions. Inoculations of this kind were commenced about 5 p.m., so that little drying out would occur during the night. Trees were left in the incubation cans for forty-eight hours, which was a sufficient period of time for ascospores to have germinated. Satisfactory humidity conditions had been maintained within the can throughout this period. When potted trees were removed from the incubation can they were transferred out of doors, where there was extremely slight or no possibility of natural infection, as no citrus trees were planted in that area for at least several miles, and then only an occasional tree in a home garden.

Negative results were obtained with the Valencia orange, kumquat and Washington Navel orange inoculations, but on Sweet Rind lemon fruits which had been inoculated in September, two out of seven showed a number of small lesions, typical of Black Spot, in March, 1939. These lesions were only several millimetres in diameter and failed to develop to any extent. One fruit was removed from the tree, the lesions aseptically removed and plated out on potato dextrose agar. The mycelium was still viable as typical colonies of *G. citricarpa* developed. No further lesions developed on the other fruits remaining on the trees, nor on any of the controls.

The following season these experiments were repeated once more at the Botanic Gardens, but, instead of making only one inoculation, four separate inoculations were carried out on four separate occasions, thus simulating the possible showers of inoculum that might occur under orchard conditions. One such inoculation was carried out shortly after petal-fall in September, another in October, another a month later, in November, and the final one just after Christmas. The same varieties were used, the same type of inoculum and the same technique. This time, as before, all varieties except the lemon failed to develop lesions. The eight small lemon fruits inoculated all developed several lesions during February. However, the few lesions which did develop must have been only a small fraction of the infections these fruits sustained. The explanation of the failure of lesions to develop on the orange fruit is most probably connected with the fact that the trees used were only five years old in 1938 and were therefore not sufficiently mature to allow development of the disease.

At Narara Viticultural Nursery during 1946 and 1947 inoculation experiments were conducted using the leaves of rough lemon seedlings. These potted seedlings were raised under quarantine conditions in the glasshouse and so were reasonably free of chance infection, and comparable controls were maintained. As in the previous

experiments, natural ascospore inoculum was used, and a similar technique employed, except that no incubation cans were available. The leaves and inoculum were merely wrapped in moist cotton wool. This proved quite adequate. No leaf lesions developed, but when inoculated leaves were removed from the seedlings, wilted and treated in the manner already described for the demonstration of latent infection, profuse development of *G. citricarpa* occurred on the dead leaves. It was found preferable to wait about six months before removing leaves that had been inoculated, as difficulty was sometimes experienced in wilting immature leaves satisfactorily. Untreated control leaves gave negative results when removed from the seedling trees, wilted and treated in the same way. Colonies of *G. citricarpa* which occurred on the dead rough lemon leaves of inoculated plants proved, on cultural examination, to be identical with the pycnidiospore form of the causal fungus of Black Spot.

These experiments with rough lemon leaves showed that the leaf primordia as they unfolded from the growing point of the stem were susceptible to infection, but that after four to five weeks or when the leaves were approximately half grown, they were no longer susceptible to infection.

Inoculations of mature Valencia fruits were carried out in a manner described by Lee (1920). The fruits were obtained from the Murrumbidgee Irrigation Area and so could be reasonably assumed to be free of latent infections. Fruits were placed in moist chambers with dead citrus leaves harbouring ripe ascospore inoculum for a week. No infections occurred. Other fruits were cut with a scalpel and small pieces of dead leaf tissue with ripe perithecia inserted. These experiments, too, failed to give any positive results. Recent experimental work aimed at controlling the disease in the orchard has shown that weak Bordeaux sprays must be applied to the young fruits in order to secure control of a disease which does not appear until twelve months later. Positive results under conditions using Lee's technique for inoculation of mature fruit would therefore have been inexplicable and contrary to field evidence. A possible explanation of the positive results obtained by Lee will be given later, when dealing with infection studies of the secondary infection cycle.

Negative, indifferent and confusing results have been obtained with closely related fungi, pathogenic on other crop plants. Reddick (1911) was unable to secure infection of grape berries with *G. bidwellii* despite the reports of successful infections by Viala et Ravaz (1888), Spechsnew (1899) and Prunet (1898). Shear, working with the cranberry scald organism *G. vaccinii*, was unable to demonstrate satisfactorily infection of the usual host plants under controlled conditions. Guba (1925), also working with a related fungus, *Phyllosticta solitaria*, was unable to demonstrate the pathogenicity of this organism to apple fruits, under controlled conditions, yet Scott and Rorer (1909) and Roberts (1917) successfully obtained infection. Later, Kohl, with the same organism, could only obtain infection if satisfactory precautions were taken to prevent the excessive drying out of the spores. This observation may have some application to the disease under discussion, but as well, with Black Spot, there is the complicating factor of latent development of the typical lesions, which make infection studies with this disease so difficult.

SECONDARY INFECTION CYCLE.

Prior to the discovery of the ascigerous fungus *G. citricarpa* on the fallen citrus leaves, and the recognition of the importance of its wind-borne ascospores as a source of inoculum, the water-borne pycnidiospores of *P. citricarpa* were regarded as the only source of infection. The coincidence of the development of this form of inoculum on the mature Valencia fruits, with the duration of the infection period on the fruit that had recently set, appeared to justify this belief. Certain anomalies existed, however. Intermediate crops of Valencia fruit set from blossoming that had occurred in March and April sometimes developed shot-hole lesions of Black Spot at maturity. Such fruit had been set, in most cases, when all the previous season's main crop Valencia fruit had been harvested. Washington Navel orange trees, reasonably isolated from other

varieties of citrus and so reasonably removed from pycnidiospore inoculum, consistently bore fruit harbouring latent infections of the Black Spot fungus. This fact was repeatedly demonstrated by the development of cultures of *G. citricarpa* on thin slices of navel orange rind tissue plated out aseptically on potato dextrose agar. No lesions develop on the Washington Navel fruits under central coast conditions, and since in any case this fruit would be harvested before the next crop was set in October, no pycnidiospores are available as a source of inoculum. The existence of latent infections within apparently healthy citrus leaves presented yet another anomaly. Such leaves are formed in early September, when pycnidiospore inoculum is not particularly plentiful, and again during March–April, when this form of inoculum is usually absent. The demonstration of abundant ascospore inoculum throughout the entire year explained satisfactorily these anomalous infections.

Pycnidiospore Liberation and Dispersal.

It now remained to discover the role of the pycnidiospore. In the spring of 1938 mature Valencia fruits were harvested with the lesions of Black Spot just commencing to appear. They were transferred to the 25°C. incubator for five days until extensive lesions had developed and abundant ripe pycnidia had appeared. This fruit was then placed under a large bell-jar through which a strong current of air was drawn. This current of air was taken into a second bell-jar, where Petri plates of acidified potato-dextrose-agar were exposed. If the pycnidiospores were air-borne some cultures of *P. citricarpa* would be expected to develop on the acidified agar. Fruit was soaked in water for periods from five minutes up to two days before submitting to test, but results were always negative, even when spore horns several millimetres in length appeared through the pycnidial ostioles. However, when such fruit, with or without spore horns, was immersed in water and that water examined under the microscope, numerous pycnidiospores were found to have escaped. The indication was that pycnidiospores were rarely if ever air-borne, but appeared to be readily water-borne.

Glycerine-coated microscope slides were exposed during the spring, summer and autumn in and near citrus orchards, to obtain some information on the amount and type of inoculum in the orchard atmosphere. This method was time-consuming and only semi-qualitative, hence in the absence of a more refined technique it can only give indications of the dispersal of these secondary spores. Fifty slides were exposed in an orchard of twenty-five year old Valencia trees, between the trees and around the boundary. During the course of the summer the fruit on these trees developed Black Spot severely, and so abundant pycnidiospore inoculum was available. Often slides had only several spores of *G. citricarpa* adhering, necessitating careful and detailed examination. Slides were prepared for examination after two days' exposure, by using a 50% solution of lactic acid as the mounting medium and a 2" × $\frac{3}{8}$ " microscope coverslip. Ascospores were observed consistently trapped on the surface of these slides but only on a very few occasions were pycnidiospores found, and then on slides exposed between trees, never on slides exposed on the boundary of the orchard. The indication was that these spores are only rarely blown about in the orchard atmosphere and then probably in water droplets. Ascospores were trapped consistently throughout the spring, summer and autumn and their numbers did not appear to be correlated with periods of rainfall. Heavier ascospore discharges could have occurred during wet spells, but the technique used was not suitable for wet weather trapping and so quantitative recordings of these periods were unreliable.

By means of a twelve-inch filter funnel and collecting bottle placed beneath a Valencia tree, portion of the dew water dripping from the tree was collected. Also in this manner portion of the incident rain in light as well as heavy showers was collected. Collections were made during the spring and summer of 1940. Water was removed, centrifuged and the deposited material examined under a microscope.

Prior to the appearance of Black Spot lesions on the maturing main crop fruit, no pycnidiospores were collected during periods of wet weather. During the period when Hard Spot lesions were developing (October) and fruit affected with these

lesions only was hanging in the trees, few pycnidiospores were found in the rain-water splashing down through the foliage into the filter funnel and collecting bottle. It was not until severe Virulent Spot lesions were developing in the trees (late November) that pycnidiospores in abundance were collected in the dripping water from the tree. At this stage it was found that pycnidiospores were plentiful in the collected water even from light rains. In the case of dews, insufficient water was collected on which an examination could be made. It is likely, however, that medium to heavy dews are sufficient to cause some spore extrusion and their washing down through the tree. When all the mature Valencia fruit had dropped from this test tree, no more pycnidiospores were detected in the water collected subsequently in the filter funnel. At this stage fallen fruit were developing pycnidia and pycnidiospores on the virulent spot lesions. Although some fruit developed Black Spot lesions early in the spring, their importance as a source of pycnidiospore inoculum does not appear to be very great. It was not until virulent lesions were being developed on fruit in the tree that pycnidiospores were numerous enough to be important as possible agencies of infection. It must be remembered that fruit affected with severe lesions of Black Spot drop readily to the ground, where their importance in providing water-borne inoculum is practically nil.

It has been observed over many years that Black Spot development is as severe on fruit at the tops as on fruit on the lower portions of the tree on the northern side. This equal distribution of the disease through the vertical plane on the northern side contrasts markedly with the distribution in the tree of another fruit disease of Valencias under central coastal conditions, namely Melanose. This disease caused by *Diaporthe citri* Wolf. is spread principally by the water-borne pycnidiospores (*Phomopsis citri*). Such spores, produced in pycnidia on the dead wood on the tree, splash down in water droplets on to the young susceptible foliage and fruit below. Hence this disease is always more serious on the fruit and foliage in the lower half as compared with that in the upper half of the tree, where the effects of the disease may be quite negligible. In the case of Black Spot, if fruit infections due to water-borne pycnidiospores were considerable, it is reasonable to assume that development would be more severe in the lower portions of the northern side of Valencia trees. However, since fruits appear to be affected just as badly in the upper portions of trees on the northern side, it tends to indicate that pycnidiospore inoculum must be regarded as of minor consequence when compared with the wind-borne ascospores.

This is in contrast to many other important fungous diseases of fruit trees. With *Venturia inaequalis* (Cke) Wint. and *Coccomyces hiemalis* Higgins, the causal organisms of Apple Scab and Cherry Leaf Spot respectively, primary infections are initiated by wind-borne ascospores, on susceptible tissues, in the early spring. These ascospores are produced in ascocarps which have overwintered in dead leaf material. The incubation period is very short for these primary infections, so that within a short time secondary spore inoculum is being produced on lesions that have formed as a result of the primary infections. Such inoculum, in the main, is water-borne and is capable of initiating a series of secondary infection cycles on susceptible plant parts, in the same season, shortly after the initiation of the primary infection cycle by wind-borne ascospores.

In the case of *G. citricarpa*, primary infections of the young leaves are initiated by wind-borne ascospores during September and October and of the young fruits during the period October to about February. Latent infections on the leaves will eventually provide ascospore inoculum to initiate primary infection cycles whenever such ever-green leaves may fall. This may be any time during a period of twelve to thirty-six months or so. Primary latent infections of the young fruits, however, will give rise to pycnidiospores when such fruits mature and develop Black Spot lesions. This may be any time from twelve to fifteen months after such fruit was originally infected. Such pycnidiospores can now initiate the secondary infection cycle. It is thus apparent that a period of twelve to fifteen months separates the initiation of

primary infections and the development of pycnidiospore inoculum for secondary infections.

Pycnidiospore Germination.

Efforts by earlier workers to obtain germination of pycnidiospores of *P. citricarpa* were not always entirely successful. Cobb (1904) recorded that these spores can be germinated only with difficulty, and Darnell-Smith (1919) found that special conditions had to be provided. He recorded that extracts of orange peel stimulated germination of freshly discharged pycnidiospores within twelve hours. However, if spores were three days old, they took several days to germinate. Spores older than this failed to germinate.

Laboratory experiments were undertaken to determine what conditions favour germination, as no quantitative studies had so far been made. Simple treatments were at first tried in efforts to secure satisfactory germination with inoculum produced under field conditions. Tap-water, incubated at various temperatures in both hanging drops and syracuse dishes, was tested without success. A few spores germinated in hanging drops, but complete failure was usually recorded in the equivalent syracuse dish tests. Later this was demonstrated to be an effect of oxygen stimulating germination of some of the spores in the outer film of the hanging drop. Normally, pycnidiospores do not germinate in water mounts, but where air bubbles are included germination of spores can be observed around them. Cobb (1904) had also seen this effect.

Since Darnell-Smith had obtained some success with orange peel extract, it was decided to test out the effect of various fruit tissues of different ages in stimulating germination. The treatments and percentage germination are set out in Table 5.

TABLE 5.

Treatments.	Percentage Germinations after 30 Hours.	
	Incubated at 20° C.	Incubated at 25° C.
Tap water	0.1	0.0
Thin section of mature Valencia orange rind in 0.2 ml. of tap water	20.9	18.2
Thin section of mature sweet rind lemon in 0.2 ml. of tap water	51.3	42.8
10 per cent. solution of ripe lemon juice in tap water	0.5	1.0
One juice sac from a ripe sweet rind lemon fruit in 0.2 ml. of tap water	60.1	43.7
Thin section of Valencia orange rind tissue from one month old fruit, in 0.2 ml. tap water ..	54.0	63.0

From Table 5 it can be seen that tissues from both young and mature fruits are capable of stimulating germination of pycnidiospores. The fact that a lemon vesicle in water was capable of exerting this effect raised the possibility that various organic acids might act as stimulants. As there was no significant difference in germination at 20°C. and 25°C., the following test was made in triplicate at 25°C., using hanging drop cultures. Details of the treatments and results obtained are set out in Table 6.

The results indicated that citric acid in concentrations from 0.5% to 0.1% was a stimulant to germination in hanging drop suspensions, but none of the other organic

acids tested had any effect on germination. The stimulation of germination by citric acid solutions appears to be independent of pH and dependent on some other unknown factor.

In subsequent work on pycnidiospore germination, erratic and inexplicable negative results were sometimes obtained with 0.1% to 0.5% solutions of citric acid. Fresh solutions of acid were prepared, but the variability appeared to be in the spore material. Pycnidiospores produced in pure culture on potato dextrose agar slopes gave particularly poor results, and it was thought that they may, under some conditions, be incapable of germination. Pycnidiospores were therefore again obtained from mature pycnidia

TABLE 6.

Treatment.	pH.	Replicate.	Number of Spores Germinated after 30 Hours.	Number of Spores Not Germinated after 30 Hours.	Percentage Germination.	Mean Percentage Germination.
0.5% citric acid.. ..	2.8	1	82	1	98.7	98.2 ± 0.70*
		2	77	2	97.4	
		3	70	1	98.5	
0.4% citric acid.. ..	2.9	1	101	41	71.1	79.6 ± 7.5
		2	140	31	81.9	
		3	108	18	85.7	
0.3% citric acid.. ..	3.0	1	77	11	87.5	86.7 ± 1.6
		2	96	13	88.0	
		3	82	15	84.5	
0.1% citric acid.. ..	3.3	1	95	14	87.2	85.0 ± 2.0
		2	60	12	83.3	
		3	141	26	84.4	
0.5% tartaric acid ..	2.8	1	1	151	0.0	—
		2	0	99	0.0	
		3	0	81	0.0	
0.4% lactic acid ..	2.8	1	0	60	0.0	—
		2	0	30	0.0	
		3	0	81	0.0	
0.5% oxalic acid ..	2.0	1	0	134	0.0	—
		2	0	115	0.0	
		3	0	129	0.0	
0.5% lemon oil ..	—	1	0	119	0.0	—
		2	0	98	0.0	
		3	0	73	0.0	
Tap water	6.8	1	0	84	0.0	—
		2	0	73	0.0	
		3	0	114	0.0	

* Expressed as standard deviations.

that had developed on mature Valencia oranges and were used in further germination trials. Even with citric acid which had given satisfactory results formerly, very disappointing results were obtained. This was surprising, since the pycnidiospores were derived from naturally occurring material, that was capable, apparently, under field conditions of causing infection.

The possibility that the age of the pycnidiospores and the conditions during spore maturation may influence germination was next investigated. A mature orange was chosen from an unsprayed Valencia tree on which severe Black Spot lesions were

commencing to develop. The fruit was placed in a closed aluminium container and incubated for six days at 25°C. By this time extensive lesions had developed and pycnidia of *P. citricarpa* were developing in large numbers. Pycnidiospores that were oozing in spore horns from ripe pycnidia were chosen for germination tests, using 0.3% citric acid solution in hanging drops. The surface of the fruit was then washed thoroughly in order to remove all pycnidiospores on the fruit surface and the greater portion of spores in the spore horns. The fruit was then submerged in tap-water for one hour at about 22°C., removed and incubated in a moist chamber at 25°C. for twenty-four hours. Germination tests were again made with the spores produced during this period. The soaking and incubation treatment was repeated for three more days.

The results of germination tests using spores collected following each period of incubation is given in Table 7.

TABLE 7.

Treatment.	Replicate.	Tap Water.		0.3% Citric Acid.	
		Percentage Germination.	Mean Percentage Germination.	Percentage Germination.	Mean Percentage Germination.
No pre-treatment (controls).	1	0.0	0.0	1.3	1.0 ± 0.9
	2	0.0		0.0	
	3	0.0		1.7	
After first 24 hours' treatment.	1	0.0	2.0 ± 2.1	5.9	10.9 ± 4.6
	2	1.7		15.1	
	3	4.2		11.8	
After second 24 hours' treatment.	1	1.2	2.7 ± 3.2	27.6	25.1 ± 2.3
	2	0.0		24.6	
	3	6.9		23.1	
After third 24 hours' treatment.	1	5.3	2.6 ± 2.6	53.5	48.0 ± 5.3
	2	2.5		42.9	
	3	0.0		47.7	
After fourth 24 hours' treatment.	1	0.0	2.3 ± 2.3	77.1	78.2 ± 4.9
	2	1.6		83.6	
	3	5.4		74.0	

It is apparent from Table 7 that germination percentage has been raised from less than 1% on the first day to 10%, 25%, 48% and approximately 80% on the second, third, fourth and fifth days respectively. These results indicate that pre-soaking of the pycnidia in water for one hour out of twenty-four has increased the percentage of spores which are capable of germinating. It would appear that fresh crops of pycnidiospores are produced and displace the spores which had been formed earlier under less favourable conditions, namely, in the absence of free moisture on and around the pycnidium for a period each day. The results of these experiments suggest that moisture conditions at the time of pycnidiospore formation influence germination ability, and that such pycnidiospores in any case are short-lived. Kohl (1932) has commented on a similar relationship between pycnidiospore maturation and moisture conditions with *P. solitaria*. However, he found that the spores of that particular fungus were much longer lived, taking up to five weeks to mature.

Under favourable laboratory conditions the pycnidia of *P. citricarpa* are capable of producing fresh crops of viable spores in a short space of time. If this is generally true, then conditions in the orchard which are suitable for rapid pycnidiospore production and maturation, namely nightly wetting of the pycnidia by dews and light rains, are also the conditions for producing pycnidiospores that will germinate readily

and infect the young fruit. From these laboratory studies it would appear that one thorough wetting is not sufficient to produce viable pycnidiospores in quantity. Daily wetting and drying appear to be necessary to produce the maximum yield of viable spores.

The mode of germination of pycnidiospores was found to be almost identical with that of the ascospores (Text-figs. 8-10). However, the pycnidiospores produce only one germ tube. Appressoria, similar in all details to those already described for ascospores, were consistently formed. Pycnidiospores germinating in 0.5% citric acid formed very short germ tubes 4μ to 8μ in length, with a distorted terminal resting spore. In the lower concentrations of citric acid used, particularly 0.1%, normal germination occurred.

Longevity of Pycnidiospores.

Darnell-Smith's observations (1919) with regard to the short-lived nature of the pycnidiospores, and the indications obtained from the experiments already reported in this paper, prompted further investigations.

Freshly matured and naturally exuded pycnidiospores were obtained from pycnidia that had developed on a ripe Valencia orange. These spores were submitted to a germination test on microscope slides, using 0.3% citric acid solution. The method adopted was as follows. Drops of water containing the pycnidiospores were placed on twelve slides and the moisture allowed to evaporate under laboratory conditions. The slides were then placed in a covered box in a laboratory cupboard. At the intervals germination trials in triplicate were conducted using 0.3% citric acid solution at 25°C. The experiment was commenced on 5th December, 1947.

TABLE 8.

Date of Test.	Replicate.	Percentage Germination.	Mean Percentage Germination.
5th December	1	70.9	79.6 ± 5.3
	2	82.4	
	3	85.6	
9th December	1	20.4	17.3 ± 2.7
	2	18.6	
	3	13.0	
5th January	1	0.0	—
	2	0.0	
	3	0.0	
5th February	1	0.0	—
	2	0.0	
	3	0.0	
5th March	1	0.0	—
	2	0.0	
	3	0.0	

From Table 8 it can be seen that after only four days' storage the mean figure for germination dropped by over 60%. No germinations were secured of spores after three months. It would appear from this experiment that pycnidiospores are very short-lived and of very little importance in the dissemination of the disease. It is not considered that pycnidiospores which may harbour in fruit cases that have carried fruit affected with Black Spot would constitute a serious source of inoculum if such cases were despatched to citrus growing areas where the disease did not occur.

Pycnidiospore Infection.

The first efforts to secure infection of citrus fruits with pycnidiospores were conducted in the spring of 1938 at the Botanic Gardens, Sydney. Similar trials already described were undertaken at that time with ascospore inoculum. The immature fruits produced by potted trees of Valencia orange, Washington Navel orange and sweet rind lemon were used for inoculation, employing much the same technique that has already been described. Naturally produced pycnidiospores on ripe Valencia fruits and pycnidiospores that had developed on the leaves of almond seedlings were used as a source of inoculum, and a check germination test was carried out with all inoculum used, to ensure that this aspect was satisfactory.

The only instance where successful infection and ultimately lesion production occurred was with sweet rind lemon fruits inoculated with spores produced on almond leaves. Four out of six fruits produced small Black Spot lesions in February, 1939. This was similar to the results already reported in trials using ascospore inoculum. It is quite possible that successful latent infections may have been established in the young Valencia fruits, although lesion development did not occur.

During the spring of 1939 infection studies were undertaken at Narara Viticultural Nursery using young fruits on fifteen-year-old Valencia trees. Pycnidiospores produced in cultures of *P. citricarpa* on sterilized Valencia rind tissue were used as inoculum. Unopened blossoms were enclosed in waxed paper bags on 25th October, 1939, to guard against the possibility of natural infection. After some of the blossoms had set fruit, wherever it was possible three small fruits on each foliage terminal were selected and tagged. Two such fruits were kept enclosed in waxed paper bags and the third was allowed to remain unprotected. This constituted a check on the susceptibility of fruits on the particular terminal in question to natural infection. Of the two remaining bagged fruits on each terminal, one was retained as a control and was kept enclosed without treatment until 18th October, 1940. The other was inoculated by the following method. The protective bag was removed and the young fruit was finely atomized with water and then with a suspension of pycnidiospore inoculum in water. Finally the interior of the bag was atomized with water and replaced over each individual fruit treated. All inoculations were carried out late in the afternoon. Originally it was intended to carry out inoculations at petal-fall, five weeks, ten weeks and finally fifteen weeks after petal-fall. Unfortunately it was not possible to carry out the petal-fall inoculations; however, the inoculations on the remaining dates were achieved. From time to time bags were removed for spraying the fruits which had been enclosed, with nicotine solution for pest control. Occasionally bags were replaced, too, when the original ones had become partly torn. The following summer, Black Spot development was not serious in the Gosford district. In fact, in many orchards the disease did not develop and in others it was very mild. This was the experience in the orchard at Narara Viticultural Nursery. The inoculated fruit was examined carefully on three occasions during the spring and summer. The results are recorded in Table 9.

From inoculated fruits developing typical lesions of Black Spot *G. citricarpa* was isolated and identified in pure culture.

Although the success of the experiment was limited because of the poor development of Black Spot generally in the spring and summer of 1940-41, some very interesting results have been obtained. The pathogenicity of pycnidiospores under field conditions was established and Koch's postulates satisfied as regards the reproduction of the disease on mature Valencia fruits. The latent nature of the infection of the causal organism was also confirmed. In one instance a particular fruit was inoculated on the 15th January, 1940, and lesion development did not occur until just prior to the 3rd February, 1941. This represents a period of about 384 days during which the infective mycelium had remained in a latent condition. It was also observed that from any given number of inoculations at different times after the fruit is set disease development tends to commence on or about the same date the following season and extend over a period of several months. This indicates that the duration of the latent

infection period is independent of the time of inoculation of the immature fruits and the time of development of the Black Spot lesions appears to be dependent, in some way, on the level of certain physiological activities in the rind of the maturing fruits rather than on the date of infection. These aspects will be discussed more fully in a later paper dealing with the epiphytology of the disease.

Attempts to infect mature Valencia fruits with pycnidiospores by the method reported by Lee (1920) were unsuccessful. The fruit for these trials, as for similar ascospore infection trials already described, was obtained from Leeton, N.S.W., where the Black Spot disease is not known to occur. It has been found that wounding the rind of sound mature Valencia fruits which harbour latent infections of *G. citricarpa*

TABLE 9.

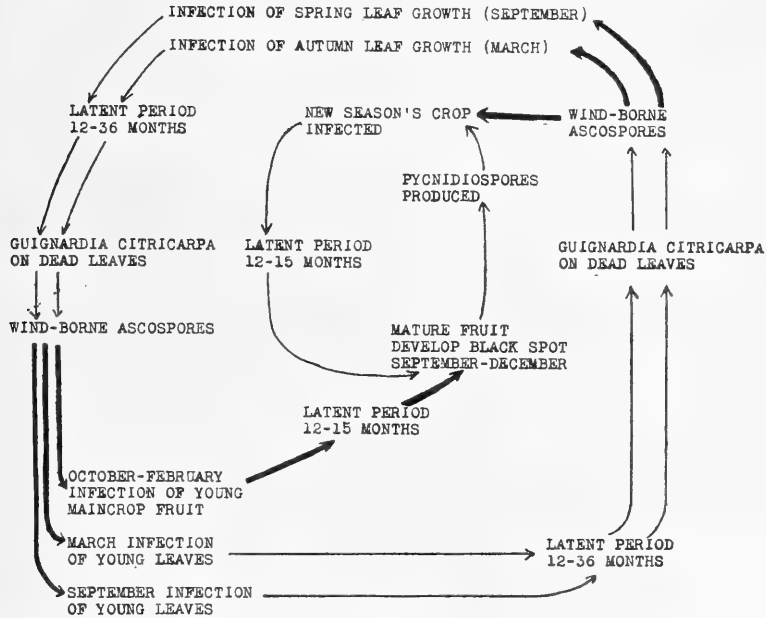
Treatment.	Number of Valencia Fruits Diseased on		
	18/10/40.	17/12/40.	3/2/41.
Inoculation 6 weeks after petal-fall 12/12/39.	$\frac{0}{17}$	$\frac{0}{17}$	$\frac{0}{17}$
Controls (bagged 25/10/39)	$\frac{0}{17}$	$\frac{0}{17}$	$\frac{0}{17}$
Natural infected (not bagged) ..	$\frac{0}{17}$	$\frac{0}{17}$	$\frac{0}{17}$
Inoculation 11 weeks after petal-fall 15/1/40.	$\frac{0}{10}$	$\frac{2}{10}$	$\frac{3}{10}$
Controls (bagged 25/10/39)	$\frac{0}{10}$	$\frac{0}{10}$	$\frac{0}{10}$
Naturally infected (not bagged) ..	$\frac{0}{10}$	$\frac{5}{10}$	$\frac{5}{10}$
Inoculation 18 weeks after petal-fall 27/2/40.	$\frac{0}{8}$	$\frac{3}{8}$	$\frac{3}{8}$
Controls (bagged 25/10/39)	$\frac{0}{8}$	$\frac{0}{8}$	$\frac{0}{8}$
Naturally infected (not bagged) ..	$\frac{0}{8}$	$\frac{4}{8}$	$\frac{4}{8}$

can result, sometimes, in the development of a typical lesion due to the activity of the mycelium of the Black Spot fungus within the rind. Spray injuries sustained by Valencia fruits, hail markings, twig abrasions and insect-damaged areas on the rind have all been observed in central coast orchards, from time to time, to be foci of lesion development. Such occurrences are especially noteworthy when they occur at a time when normal lesion production has not commenced on undamaged Valencia fruits. It may have been quite possible that in using mature fruit for inoculation Lee damaged the rind of fruits harbouring latent infections, and in this way secured some lesions which could have been the result of the activity of latent mycelium.

SPREAD OF THE DISEASE BY NURSERY TREES.

Using the technique described for the detection of the presence of latent infections, it has been found that these occur very abundantly in the leaves of nursery trees from commercial nurseries at Carlingford and Gosford, and from the Narara Viticultural

Nursery. This raises an important issue. In a suitable environment mature ascospores of *G. citricarpa* can develop on these infected leaves after they are shed. Thus the possibility arises of these nursery trees being able to carry the disease with them into areas where it does not at present occur. Though the amount of latent infection may be considerable in the green leaves, such nursery trees, when inspected by the nurseryman, orchardist, plant disease inspector or plant quarantine officer at the despatch depot, would appear to be quite free of disease. In this manner the disease could also be introduced from a country where the disease occurs to a citrus-growing area in another country where the disease does not occur. It seems most unlikely, from the evidence already presented, that spraying the yearling trees with protective Bordeaux Mixture applications would prevent infection. Hence the movement of trees raised in citrus areas where the Black Spot disease occurs to other citrus-growing areas which are free of this disease must be a practice accompanied with considerable risk. It will be shown in a later paper on the epiphytology of this disease that latent infection can only take place when certain conditions of the environment occur, and that other conditions again are necessary for the latent infections to develop into lesions on the fruit. But in spite of this it would seem desirable for new plantings in those citrus areas which are at present free of this disease to be made with locally



Text-fig. 11.—The complete cycle of infection, including both the primary (ascospore) and the secondary (pycnidiospore) cycles.

grown trees. Failing this, and where nursery tree requirements continue to be fulfilled from areas where the disease does occur, the most satisfactory alternative would be for the nurseryman to strip off all leaves and petioles (which also harbour latent infection) and to despatch trees immediately in this condition. In this manner all of the latent mycelium would be removed and there would be very little danger of introducing the disease. Such a practice would not, however, be very acceptable either to the nurseryman or the citrus growers, who have always preferred to take delivery of trees with satisfactory foliage cover.

For many years now young trees have been despatched from nurseries on the coast of New South Wales where Black Spot occurs, to the inland areas where the disease does not occur, and despite the continual introduction of the inoculum in a latent form, the disease has been reported only very rarely. There is one record in

the files of the Biological Branch, Department of Agriculture, of the disease on Valencia orange fruits at Barooga, on the Murray River, and one from the same locality of its occurrence on lemon fruits. The examination and identification was made by Mr. F. C. McCleery, at that time Plant Pathologist. There is also one record of specimens of lemons from Curlwaa, also on the Murray River, 250 miles west of Barooga.

During the winter of 1941 an extensive survey was made of the citrus orchards of the Murray River area as far west as Kerang. A large number of specimens of dead leaves were collected for examination in the laboratory and green leaves were removed from the trees in the hope that some evidence of the latent mycelium of the causal fungus might be obtained. No trace of *G. citricarpa* was found.

Shortly after this, specimens of green leaves from Valencia orange trees were obtained from Leeton, on the Murrumbidgee Irrigation Areas. Ninety-one leaves were treated for the development of latent infections. After seven days one leaf showed copious development of spermogonia of *G. citricarpa*. Apparently some limited quantity of inoculum is produced from time to time in this region and a very limited amount of infection occurs on the green leaves. Whether such infections are able to occur on the young fruits is questionable, as conditions favourable for infection are unlikely to occur in the Murrumbidgee Irrigation Areas from October onwards. The disease has not so far been recorded on fruit from the Murrumbidgee Irrigation Areas.

In the early summer of 1947 a survey was made of citrus trees in the Murrumbidgee Irrigation Areas. As in the previous survey, both dead and green leaves were collected. No evidence was obtained that latent infection of *G. citricarpa* was present. Shortly afterwards a survey was made of orchards on the lower Murray River at Mildura, Merbein, Redcliffs, Curlwaa, Coomealla, Mallee Cliffs and Pomona. Samples similar to those already described were collected and examined. However, no evidence was obtained that *G. citricarpa* was present in any of those areas.

APPENDIX.

STANDARD TECHNIQUE FOR DEVELOPMENT OF LATENT MYCELIUM WITHIN CITRUS LEAVES.

The standard technique finally adopted for the testing of green citrus leaves for the presence of latent mycelium of *G. citricarpa* is as follows. This procedure is suggested when it is suspected that the Black Spot disease may be present in an area in a latent form. Leaves of sweet rind lemon and of Valencia orange or of grapefruit should be chosen. Such leaves should be at least one year old or in their second year of maturity. In testing either grapefruit or Valencia orange leaves it is desirable always to conduct a parallel test with leaves from lemon trees if they are available in the area. Leaves should be exposed out of doors in direct sunlight. It has been found convenient to place them in flat wire gauze containers. The period of exposure should be from six to twelve hours, or until the leaves have assumed a mid-brown to pale brown colour, but are still devoid of any definite brittleness. Following this treatment the leaves should be dipped in 70% alcohol for several seconds and then immersed in 1 in 1,000 mercuric chloride solution for ten minutes. The leaves should then be washed well in sterilized water and removed to a second container of sterilized water, in which they are allowed to soak for half an hour. The leaves should then be removed, the excess water drained off, and the leaves placed in a suitable dish in a 30°C. incubator until the following afternoon, when the leaves are taken from the incubator, immersed once more in sterilized water for half an hour, removed and the excess water again is allowed to drain off. The leaves should not be returned to the 30°C. incubator until the following morning. Repetition of this treatment daily should bring about the development of any latent mycelium of *G. citricarpa* in seven to eight days.

In exposing citrus leaves that have been removed from the tree, local environmental conditions should be taken into account. If the tests are made in hot weather with temperatures in the sun around 100°F. at midday and with a high saturation deficit

of the order of 1.00 in. of Hg., then the exposure of citrus leaves for a twelve-hour period would result not only in the rapid dehydration and death of the leaves, but also of the latent mycelium of *G. citricarpa* within. Under such conditions an exposure of six hours would probably be ample to ensure sufficient wilting without killing the latent mycelium to any considerable extent. When leaves from orange or lemon trees have been exposed for the purpose of wilting they should have a mid-brown to pale brown appearance, be just pliable but not brittle. The bleaching of the colour from exposed leaves is perhaps the most reliable indication that the exposure period has been too long or is approaching the danger point. Once leaves lose their mid-brown to pale brown colour and begin to assume a pale biscuit-beige hue the danger point is being reached. Usually at this stage the leaves are brittle and the latent mycelium of *G. citricarpa* has been killed.

The duration of immersion in cold water after exposure to ensure proper development of the Black Spot fungus is a matter of empirical choice and permits considerable latitude. A half-hour was chosen, as it was found that exposed leaves had absorbed their maximum amount of water from an immersion of this duration. It was also found that where leaves were given longer daily periods of immersion a certain amount of dissolution of the dead citrus leaf tissues took place, making them difficult to handle. It has been observed that where initial exposure has not been sufficiently long to ensure a satisfactory growth of *G. citricarpa* the dying leaves, upon being immersed in water, are able to imbibe considerable amounts. With increased exposure this ability to imbibe water is largely lost, until in the instance of over-exposed leaves the tissues still remain fairly brittle after half an hour's immersion in water. Exposure and wilting of citrus leaves apparently destroy the imbibing properties of the colloidal materials of the cells. This may only be an indication of the death of these cells. Should this process be taken too far the latent mycelium of *G. citricarpa* itself is apparently destroyed, as such leaves do not, and cannot be, induced to develop growth of *G. citricarpa* in any of its forms.

SUMMARY AND CONCLUSIONS.

1. Studies of Black Spot of Citrus on the Central Coastal District of New South Wales have been in progress for a number of years.

2. The history of the disease, its occurrence throughout the world, and its importance as the most serious disease affecting citrus on the East Coast of New South Wales, have been surveyed.

3. A description of the disease has been presented, and the different types of lesions on Valencia fruits, as the season progresses, have been classified. The disease does not appear to develop seriously until the fruit is approaching maturity. Occasionally small lesions are observed on lemon foliage, only very rarely on orange foliage. Evidence on the latent infection nature of the disease has been presented.

4. In an isolated orchard complete removal of diseased Valencia fruits harbouring pycnidiospore inoculum, prior to the setting of the new season's fruit, failed to give control of Black Spot the following season. An alternate source of inoculum was suspected.

5. Pycnidia, spermogonia and pycnidio-sclerotia of *Phoma citricarpa* have been found to occur on dead leaves of Citrus, to a very great extent under orchard conditions, on the East Coast of New South Wales.

6. Also occurring on old dead citrus leaves was an undescribed ascigerous fungus. Its relationship with *P. citricarpa* has been established, and on the grounds of its conformity with the type genus *Guignardia*, this sexual stage has been named *Guignardia citricarpa*, and the fungus described.

7. Histolysis of the pseudoparenchyma in the pycnidium has been discussed with relation to its importance. The gelatinous appendage to the pycnidiospore appears to be derived from the histolysis of this tissue.

8. The relationship of *P. citricarpa* McAlp. to the genus *Phyllostictina* Syd., as emended by Shear, has been demonstrated. Further work is necessary on this group, however, to establish satisfactorily the validity of Shear's concept, before any reclassification could be possible.

9. In addition to its occurrence on all species and varieties of Citrus, *G. citricarpa* has been shown to occur as latent infections on the leaves of a number of native bush shrubs and cultivated plants belonging to nine different natural families.

10. The development of *G. citricarpa* on surface sterilized dying Citrus leaves has been demonstrated to have originated from latent infections that were present in the green leaves on the tree, and not as a true saprophytic growth of this fungus on the leaves after their death.

11. Wilting of the green citrus leaves by exposure to the sun after removal from the tree greatly increased the chances of such leaves developing the various fructifications of *G. citricarpa*. Alternate wetting and drying of these leaves also favourably influenced the development of these fructifications.

12. The maturity of Citrus leaves greatly influenced the result obtained by "wilting" after removal from the tree. Young leaves, of only a few months' maturity, required much longer periods of exposure to achieve the development of fructifications of *G. citricarpa* from latent mycelium.

13. It has been demonstrated that *Colletotrichum gloeosporioides* occurs also as a latent infection in Citrus leaves, under Central Coastal conditions; however, wilting of the leaves is not necessary in order to secure the development of acervuli of this fungus on the dying leaves.

14. Latent infections of *G. citricarpa* have been demonstrated to survive eighteen days in wilted air-dried citrus leaves, and then produce fructifications when such leaves were moistened. The possible adaptation of this fungus to semi-arid conditions has been demonstrated.

15. Conditions favourable, and unfavourable for ascocarp maturation have been demonstrated and discussed. The importance of alternate wetting and drying of the dead leaves in order to secure ripe perithecia has been outlined. Mature ascospores were developed three to four months after the leaves were removed from the tree.

16. The importance of evening dews in providing a means of wetting the dead citrus leaves and so ensuring the plentiful production of ascospores has been discussed.

17. Bordeaux Mixture spray deposits on Citrus leaves in no way interfered with the ability of such leaves as they died to develop fructifications from latent mycelium.

18. After ten years' protective spraying of Valencia trees in a particular orchard, with recommended strengths of Bordeaux Mixture, Black Spot disease was just as serious, and inoculum just as plentiful as ever.

19. Foliage protection sprays with Bordeaux Mixture proved to be unsuccessful in preventing infection of leaves.

20. Older citrus trees provide a more reliable source of inoculum from their dead leaves than very young trees. More favourable conditions for maturation of ascocarps are provided by the shelter of larger trees. Young trees, however, do provide some inoculum from their dead leaves.

21. Latent mycelium of *G. citricarpa* has been demonstrated in the green leaves of citrus yearling trees, in commercial nurseries, and fructifications developed on the dead leaves from such yearling trees.

22. A standard technique has been presented for the possible demonstration of latent mycelium of *G. citricarpa* in apparently "healthy" citrus leaves, in areas where the disease in a latent condition may be suspected.

23. The fruit on young Valencia trees does not develop Black Spot at maturity, although such fruit has been demonstrated to harbour latent mycelium. It is possible for the orchard to become infected and the life cycle of the fungus continue for some years, without the development of macroscopic lesions.

24. Citrus leaves have been shown to harbour mature ascospores throughout the entire year.

25. Ascospores are ejected from the perithecium with explosive violence, and are air-borne.

26. Ascospores germinate without the necessity of special conditions; after forty-eight hours 70% had germinated.

27. An appressorial body, or resting spore is produced terminally on the germ-tube of the germinating ascospore.

28. Infection studies with ascospores proved their pathogenicity on young lemon fruits, and young rough lemon foliage.

29. Negative results were obtained with inoculations of mature Valencia fruits, known to be free from latent infections.

30. The liberation and dispersal of pycnidiospores have been studied and the importance of their water-borne nature discussed.

31. The relationship of the primary life cycle to the secondary life cycle of the causal fungus has been studied and discussed.

32. The oxygen requirements of germinating pycnidiospores have been observed, and the importance of dilute citric acid solutions in stimulating germination studied.

33. Pycnidiospores lose their viability rapidly, failing to germinate one month after they were produced.

34. The infective nature of pycnidiospores has been demonstrated in the orchard and in the glasshouse on young Valencia and young lemon fruits.

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EXPLANATION OF PLATES.

PLATE XV.

Fig. 1.—Three mature Valencia oranges, on which lesions of "Hard Spot" have developed. Note the green "halo" around the restricted lesions. Fruit collected during September.

Fig. 2.—Mature Valencia orange with "Hard Spot" lesions of Black Spot. Even though some lesions are adjacent, they do not coalesce, as the causal fungus is most probably dead. Fruit collected during October.

Fig. 3.—"Hard Spot" lesions on a mature Valencia orange. Note the variation in the size of the individual lesions.

Fig. 4.—Eureka lemon fruit with one irregular "virulent" lesion and one smaller virulent lesion. Note the "Hard Spot" lesions which have not developed any further, and which will be "engulfed" by the larger virulent lesion.

PLATE XVI.

Fig. 1.—Eureka lemon fruit with multiple development of "Hard Spot" lesions.

Fig. 2.—"Freckle Spot" development on a maturing Duncan grapefruit. Note the intensity of development of the lesions. At the time the photograph was taken lesions were continuing to develop from latent infections.

Fig. 3.—A mature Eureka lemon fruit on which a multiple development of "Freckle Spot" lesions has been followed by the development of a virulent lesion at "a".

Fig. 4.—Mature Valencia orange fruit showing "Hard Spot" lesion at "a", being engulfed by the development of a "virulent" lesion "d". An isolated "Hard Spot" lesion at "a". Five "virulent" lesions growing together at "b", and a recently appeared virulent lesion at "c".

PLATE XVII.

Fig. 1.—Two mature Valencia orange fruits developing "Virulent Spot" lesions. Note the tendency for the rapidly growing lesions to become confluent. New virulent lesion commencing to develop at "a". Fruit collected during late December.

Fig. 2.—Two Valencia orange fruits with early stage of "Virulent Spot" lesions.

PLATE XVIII.

Fig. 1.—Two mature Valencia orange fruits showing "Freckle Spot" lesions at "a", "Hard Spot" lesions at "b", "Virulent Spot" lesions at "c", and "Hard Spot" lesions at "d", being engulfed by the growth of the "virulent" lesion.

Fig. 2.—Two Valencia orange fruits with "Hard Spot" lesions at "a" and on which at a later date isolate virulent lesions have developed at "b".

Fig. 3.—Mature Valencia orange fruit showing "Hard Spot" lesions at "a" about to be engulfed by the activity of the "virulent" lesion "c" which has involved more than half the fruit's surface. "Hard Spot" lesions at "b" that have been overgrown by the virulent lesion. "Freckle Spot" lesions at "d". Smaller virulent lesion developing at "e".

Fig. 4.—A collection of Valencia orange fruits, a typical sample gathered from unsprayed trees during an epiphytotic.

PLATE XIX.

Fig. 1.—Eureka lemon leaves, ventral surfaces with Black Spot lesions. Note the pycnidium in the lesion of "a". a and b, ventral surfaces. c, same Eureka lemon leaves as in a and b dorsal surfaces.

Fig. 2.—Enlargement $\times 2$ of dead lemon leaf, showing ripe perithecia of *G. citricarpa*.

PLATE XX.

Fig. 1.—Two dead Valencia orange leaves with a profuse development of ripe perithecia of *Guignardia citricarpa*. Note the appearance of leaves harbouring mature ascospores.

Fig. 2.—Dead leaves harbouring perithecia, collected from beneath citrus trees, usually have a twisted or rolled shape when dry.

Fig. 3.—Dead leaf of Smilax (wild sarsaparilla), showing pycnidia of *P. citricarpa* developing on the ventral surface.

Fig. 4.—Lemon leaf, ten days after wilting treatment, with only scanty development of *P. citricarpa*. The leaf was allowed to dry out during the period it was in the incubator.

Fig. 5.—Dead lemon leaf, showing the effect of insufficient wilting on the subsequent development of organisms from latent infections. *P. citricarpa* has developed at "a" and *Colletotrichum gloeosporoides* has developed at "b".

Fig. 6.—Dead lemon leaf, showing the failure of *P. citricarpa* to develop in the area around "a" while developing satisfactorily on the remainder of the leaf tissue. Tissue at "a" was apparently over-exposed during the wilting treatment, resulting in the death of the latent mycelium of *G. citricarpa* within the tissue.

Fig. 7.—Dead leaf of Valencia orange, ten days after removal from the tree. The leaf has failed to develop spermogonia of *G. citricarpa* from latent mycelium after initial wilting treatment, owing to failure to moisten leaf sufficiently after exposure.

PLATE XXI.

Fig. 1.—Dorsal surface of waratah leaf eight days after removal from the bush, showing the development and coalescing of the colonies of *P. citricarpa*.

Fig. 2.—Same leaf as in Fig. 3, ventral surface. Note pycnidia developing in the discrete lesions.

Fig. 3.—Dead Turpentine leaf, dorsal surface showing lesions "a" of Black Spot that developed when the leaves were alive on the tree, and pycnidia at "b" that have developed after the death of the leaves. Lesions at "a" develop as the result of injury to the leaf following egg deposition by a species of psyllid.

Fig. 4.—Ventral surface of Waratah leaf (dead), with development of pycnidia of *P. citricarpa*.

Fig. 5.—Dorsal surface of dead Waratah leaf (three months) with maturing perithecia of *G. citricarpa*.

Fig. 6.—Dead leaf of Camellia, dorsal surface, with pycnidial development of *P. citricarpa*.

STUDIES ON AUSTRALIAN MARINE ALGAE. IV.

FURTHER GEOGRAPHICAL RECORDS.

By VALERIE MAY, M.Sc. (C.S.I.R., Marine Biological Laboratory, Cronulla, N.S.W.)

[Read 29th September, 1948.]

INTRODUCTION.

A. H. S. Lucas in 1909 and 1912 published lists of the brown, red and green marine algae then known to occur in Australian waters, together with their distribution in this area. Since these dates relatively few additions to our marine flora, or extensions of geographical ranges here, have been recorded. In the present series of papers May (1945, 1946) has reported the occurrence of species previously not known from Australia, together with records extending the geographical ranges of other species here. The present paper contributes further to these records. Unless stated otherwise, the specimens quoted are located either in my own herbarium (quoted as V.M.) or in the National Herbarium of New South Wales (quoted as N.S.W.).

MYXOPHYCEAE.

HORMOTHAMNION ENTEROMORPHOIDES Grun. ex Born. & Flah.

New Record for Australia.

Dr. Francis Drouet, of the Chicago Natural History Museum, kindly identified this species for me. The genus has not previously been recorded from Australia.

Locality:	Date.	Herbarium.	Notes.
Hayman Island, Queensland.	-/8/1946	V.M. No. 2403 and Herb. Univ. Syd.	From high and low reef flat, and from deep moat surrounding island. Coll. Mrs. Bingham.

MELANOPHYCEAE.

CHNOOSPORA PACIFICA J. Ag.

New Record for Mainland of Australia.

Setchell and Gardner (1925) showed that *Chnoospora fastigiata* J. Ag. should rightly be called *C. pacificia* J. Ag. Under the former name De Toni and Forti (1923, p. 80-1) had recorded the occurrence of this species in Tasmania. The present is the first record of the species from the mainland of Australia. The specimen agrees with Harvey's Algae of Ceylon No. 60 (Nat. Herb., N.S.W.).

It is indeed surprising that this species should be missing from, or have escaped detection in, the coast area between these two Australian localities.

Locality.	Date.	Herbarium.
Caloundra, Queensland.	23/1/1944	V.M. No. 965.

RHODOPHYCEAE.

SCINAIA MONILIFORMIS J. Ag.

New Record for New South Wales and Lord Howe Island.

A description and illustration of this species was given by Setchell (1914) and is the basis of the present identification. The type specimen is from Port Phillip Heads, Victoria, and the present is the first record of the species from New South Wales and also from Lord Howe Island.

This species, with its regularly constricted thallus, appears to have been mistakenly identified as *Colearthrum Muelleri*, which is superficially similar in habit, but differs very much in the microscopic structure as shown in transverse section. Lucas (1914, p. 462) recorded *C. Muelleri* (as *Erythrocolon Muelleri*) as occurring at Botany Bay, N.S.W.; however, since specimens from Botany Bay in the National Herbarium, N.S.W., labelled by Lucas as *Erythrocolon Muelleri* were in fact *Scinaia moniliformis*, it appears likely that the record of *C. Muelleri* from New South Wales is based on mistaken identity.

Locality.	Date.	Herbarium.	Notes.
Collaroy, near Sydney, N.S.W.	2/ 4/1944	V.M. No. 253	Drift.
" " " "	7/ 2/1945	V.M. No. 347	"
" " " "	8/12/1945	V.M. No. 1182	"
" " " "	19/12/1944	V.M. No. 467	"
Botany Bay, " "	-/ 6/1910	N.S.W.	Coll. A. H. S. Lucas
" " " "	-/ 6/1903	N.S.W.	" "
" " " "	-/ 1/1912	N.S.W.	" "
Lord Howe Island	—	N.S.W.	" "

GLOIOPHLOEA SCINAIOIDES J. Ag.

New Record for Tasmania.

In the National Herbarium of N.S.W. there is a herbarium specimen collected at Stn. 5, Port Phillip Heads, Victoria, by J. Br. Wilson on 31/12/1888; this specimen agrees with the illustration and description of *G. Scinaoides* given by Setchell (1914), comes from near the type locality (Western Port, Victoria) and is considered as representing that species.

This species is now recorded from Tasmania.

Locality.	Date.	Herbarium.	Notes.
River Tamar, Tasmania.	-/3/1932	N.S.W.	Coll. F. Perrin and A. H. S. Lucas

PSEUDOSCINAIA AUSTRALIS Setch.

New Record for New South Wales and for Tasmania.

Setchell (1914) described and illustrated this species with the type locality Port Phillip Heads, Victoria. The present records extend the known distribution of this species to both New South Wales and Tasmania, while the writer has found traces of the plant in Hervey Bay, Queensland (Aug., 1943).

P. Australis is rather similar in habit to *Gloiophloea Scinaoides*, also mentioned in the present paper, but differs in that the structure of the peripheral layers as shown in transverse section is that of a *Scinaia*. Further, *G. Scinaoides* is a softer, finer plant with more imbricate branching.

Locality.	Date.	Herbarium.	Notes.
Collaroy, near Sydney, N.S.W.	24/11/1945	V.M. No. 1153	Drift.
" " " "	8/12/1945	V.M. Nos. 1180-1	"
" " " "	21/ 1/1946	V.M. No. 2015	"
Uranga, N.S.W.	26/ 9/1943	V.M. No. 2182	"
River Derwent (near mouth), Tasmania.	-/ 1/1911	N.S.W.	Coll. L. Rodway.

PTEROCLADIA CAPILLACEA (Gmel.) Born. & Thur.

New Record for Western Australia.

This species is known from the east coast of Australia from Victoria to Queensland. It occurs, generally in large quantities, on rocky headlands near low-tide level. The present appears to be the first record of it from Western Australia.

Locality.	Date.	Herbarium.	Notes.
Longreach Bay Reef, Pt. Peron, Western Australia.	22/11/1946	V.M. ex Herb. Univ. W.A.	Growing in dense clumps in upper levels of cleft. Coll. G. Smith (No. 110).
Carnac Island, near Fremantle, Western Australia.	30/ 3/1935	Herb. Univ. W.A.	The upper portions of the fronds of this specimen are finer than is usual for the species. Coll. F. B. Nairn.

Mr. G. Smith, of the University of Western Australia, tells me that this species is quite common in the Perth coastal area, occurring also at Rottneest and Cottesloe.

RHABDONIA NIGRESCENS HARV.

New Record for New South Wales and for Queensland.

This species was distributed by Harvey as Alg. Aust. Exsicc. No. 389 from Georgetown, Tas., a specimen of which was examined from the National Herbarium, N.S.W.

R. nigrescens has been recorded previously from Tasmania and from the southern coast of Australia; it is now recorded from the eastern shores of the continent, where

it appears to be moderately prevalent. It seems that this species has in the past been confused locally with the finer form of *Gracilaria confervoides*, which it resembles in habit, but from which it is readily distinguished by the structure of the thallus as shown in transverse section. *Solieria robusta* resembles *R. nigrescens* in thallus structure, but is larger and differs in the structure of the cystocarp.

Locality.	Date.	Herbarium.	Notes.
Inskip Point, Sandy Straits, near Maryborough, Queensland.	26/ 8/1943	V.M. No. 2176.	Trawled. Cystocarpic.
Two Gutters, Hervey Bay, near Maryborough, Queensland.	25/ 8/1943	V.M. No. 2177.	" "
Macleay Island, Moreton Bay, Queensland.	7/ 3/1945	V.M. No. 590.	" "
Canaipa Passage, Moreton Bay, Queensland.	7/ 3/1945	V.M. No. 581	
Dunwich to One Mile, Stradbroke Island, Moreton Bay, Queensland.	6/ 3/1945	V.M. No. 591.	Sandy bottom.
Collaroy, near Sydney, N.S.W.	2/ 4/1944	V.M. No. 251.	Drift.
" " " "	15/10/1944	V.M. No. 165.	" Cortex thin.
Middle Harbour, Pt. Jackson, N.S.W.	4/12/1944	V.M. Nos. 237 and 239.	Trawled.
Farm Cove, Pt. Jackson, N.S.W.	-/ 7/1901	N.S.W.	Plant as <i>Gracilaria confervoides</i> . Coll. A. H. S. Lucas.
" " " "	6/ 7/1944	V.M. Nos. 1133 and 1135.	Trawled.
Botany Bay, N.S.W.	- / 3/1944	V.M. No. 1134.	
" " " (Towra).	24/ 3/1944	V.M. No. 304.	Drift.
" " " "	15/ 3/1944	V.M. No. 1136.	Trawled. Tetrasporic.
" " " "	10/ 9/1943	V.M. No. 1138.	" "
" " " "	20,10/1943	V.M. No. 1137.	" "
Port Hacking, N.S.W.	7/ 8/1944	V.M. Nos. 101 and 102.	On shells.
Lake Illawarra, N.S.W.	-/ 9/1944	V.M. No. 123.	
Kanahooka Point, Lake Illawarra, N.S.W.	24/ 3/1945	V.M. No. 635.	In tussocks.

MELANTHALIA OBTUSATA (Labill.) J. Ag.

New Record for New South Wales.

M. obtusata is illustrated by Harvey (1858-63, Pl. 25), who describes the great variability which may occur in the thallus width of this species. Both the normal form and the narrow var. *intermedia* Harv. have now been collected from the eastern coast of Australia, though both are previously recorded as only from the south coast and from Tasmania.

Locality.	Date.	Herbarium.	Notes.
Tuggerah Lakes, N.S.W.	-/ 4/1911	N.S.W.	Coll. A. H. S. Lucas. Previously identified as <i>Trematocarpus concinnus</i> (R.Br.) J. Ag.
Boat Harbour, Tuggerah, N.S.W.	10/ 2/1943	V.M. No. 2198.	
Collaroy, near Sydney, N.S.W.	30/ 5/1944	V.M. No. 263.	Drift.
" " " "	2/ 4/1944	V.M. No. 257.	" "
" " " "	15/ 7/1944	V.M. No. 390.	" "
" " " "	16/ 6/1945	V.M. No. 873.	" "

CURDIEA LACINIATA Harv.

New Record for New South Wales.

This species was illustrated by Harvey (1858-63, Pl. 39) and his Alg. Aus. Exsicc. No. 303 (from Port Phillip Heads, Vic.) was examined by the writer in the National Herbarium, New South Wales.

Known previously from the southern coasts of Australia and from Tasmania, this species has now been found as drift in New South Wales.

The cystocarps of this species are not limited to the margins, as illustrated by Harvey, but occur also on the flattened parts of the thallus.

Locality.	Date.	Herbarium.	Notes.
Collaroy, near Sydney, N.S.W.	15/7/1944	V.M. No. 392.	Drift. Cystocarpic.
" " " "	8/6/1945	V.M. No. 869.	Drift. Tetrasporic.

CURDIEA CRATERIFORMIS (J. Ag.) Kylin.

New Record for Australia.

The type specimen of this New Zealand species is illustrated by Kylin (1932), Taf. 25, fig. 61.

A specimen from Paihia, New Zealand, collected 24/7/1938, and kindly sent me by Mr. V. W. Lindauer, was also available for examination.

The Australian specimens are very coarse and leathery. They were all obtained as drift following heavy seas.

Locality.	Date.	Herbarium.	Notes.
Collaroy, near Sydney, N.S.W.	30/5/1944	V.M. No. 269.	
" " " "	18/6/1945	V.M. No. 862.	Cystocarpic.
Kiama, N.S.W.	23/6/1945	V.M. No. 830.	

HYMENCLADIA USNEA (R. Br.) J. Ag.

New Record for New South Wales.

This species occurs moderately frequently on the Victorian coast, so that it is not surprising that it should occur on the south coast of New South Wales.

The New South Wales plants agree reasonably with Harvey's specimen of *H. usnea* (Alg. Aus. Exsicc. No. 365), which was examined from the National Herbarium, New South Wales; this species is also illustrated by Harvey (1858, Pl. 118).

Locality.	Date.	Herbarium.	Notes.
Tathra, N.S.W.	31/1/1943	V.M. No. 2186.	
" " "	31/1/1943	V.M. No. 2209.	Smaller specimen.

ACANTHOPHORA DENDROIDES HARV.

New Record for New South Wales.

This species (represented by Harvey's Alg. Aus. Exsicc. No. 139 in the National Herbarium, N.S.W.) was known only from the south-west of Australia until in 1912 Bailey (p. 825) recorded it also from Queensland. The present report extends the distribution to New South Wales also.

Locality.	Date.	Herbarium.	Notes.
Port Stephens, N.S.W.	-/3/1913	N.S.W.	Cystocarpic.

EUZONIELLA INCISA (J. Ag.) Falk.

New Record for Eastern Australia.

This species is known from the western and southern coasts of Australia and from Tasmania, and is now recorded from New South Wales. The habit of this genus is distinctive, since the ultimate ramuli are borne on the upper sides of alternate branches. This species appears to be fairly prevalent in New South Wales, and the fact that it has not previously been reported from this coast is probably due to its small size.

Locality.	Date.	Herbarium.	Notes.
Eden, N.S.W.	-/ 1/1910	N.S.W.	A small collection made by A. H. S. Lucas.
Barrenjoey Head, Broken Bay, near Sydney, N.S.W.	25/ 2/1945	V.M. No. 518.	On <i>Sargassum</i> sp.
Pittwater, near Palm Beach, near Sydney, N.S.W.	10/12/1945	V.M. No. 1176	Trawled.

Traces of this species have also been found at the following N.S.W. locations:

Merrywether Beach, Newcastle.	18/12/1942
Tathra.	3/ 1/1943
Port Hacking.	12/10/1943

EUZONIELLA FLACCIDA (Harv.) Falk.

New Record for Eastern Australia.

This species differs from *E. incisa* by being a softer, slenderer plant with its ultimate ramuli usually monosiphonous instead of polysiphonous. *E. flaccida* is known from the western and southern coasts of Australia, but the present is the first record of it from the east coast.

Locality.	Date.	Herbarium.	Notes.
Redcliffe Beach, Moreton Bay, Queensland.	28/5/1943	V.M. No. 560.	Drift.

EUZONIELLA HARVEYANA (Decne.) Falk.

New Record for Victoria.

This species is larger and coarser than is *E. incisa*. It has been recorded previously from Tasmania and from New Zealand, but the present record is the first for the mainland of Australia.

Locality.	Date.	Herbarium.	Notes.
Barwon Heads, Victoria.	-/2/1932	N.S.W.	Coll. Jessie Brooks.

SPECIES EXCLUDENDAE.

As discussed under *Scinaia moniliformis*, *Colearthrum Muellerei* (Sond.) Borgs. is to be excluded from the records of species of algae occurring in New South Wales.

SUMMARY.

In this paper *Hormothamnion enteromorphoides* and *Curdiea crateriformis* are recorded for the first time from Australia. There are also reported a number of collections which extend the known geographical range of other species within Australian waters.

Colearthrum Muellerei is excluded from the algae known from New South Wales.

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MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. XIV.

VENATION AND OTHER NOTES.

By G. H. HARDY,
University of Queensland, Brisbane.
(Six Text-figures.)

[Read 29th September, 1948.]

INTRODUCTION.

Concerning his association with the Comstock system of venation, Needham (1908, p. 219) wrote: "He once told me that it was in the study of the venation of the Diptera that he first felt the solid ground of true homologies beneath his feet. I have had hitherto no share in the brilliant work that has been done on the venation of the order. The chapters on Diptera, Hymenoptera and Lepidoptera of the *Wings of Insects* were wholly the work of Professor Comstock. After this work was done I joined in the search for ontogenetic confirmation of homologies already determined; but in the order Diptera that search proved wholly fruitless. The proof of homologies in dipterous venation rests on comparative anatomy alone."

In addition, Needham, in the same work, showed some weaknesses of the system applied to Diptera, and since then it has become generally assumed that the notation R_5 has been applied incorrectly throughout the order. This accounts for various papers appearing still clinging to the Comstock system and yielding some seemingly fantastic notations, based on evidence more or less acceptable, such as the Vignon and Séguy system, upon which Captain E. Rivenhall Goffe (1947) has given an excellent rendering based upon the Syrphidae.

A danger is recognized in the modern trend for taxonomists to develop their own hybrid notation in bewildering variety based upon the systems of Comstock-Needham, Tillyard, Alexander, Shannon-Bromley and Vignon-Séguy. The present endeavour to find a pathway through all this basic work brings forward yet another aspect of the problem, one that gives hope of solving those numerous anomalies left in the train of the views applied by the various authors mentioned above.

It seems now that tracheation, laying down the original wing venation, disappeared when numerous veinlets formed a meshwork especially over the apical half of the wing. Basally of the furcation of the concave median vein (MP), Needham discovered in Tipulidae five "supernumerary" veins and ten beyond that point, this leading him to the view that "a more or less irregular meshwork of cross-veins disappeared in the progressive differentiation between strong veins and thin membrane". The concrete evidence of this theoretical meshwork, unknown to Needham, occurs in certain African Nemestrinidae.

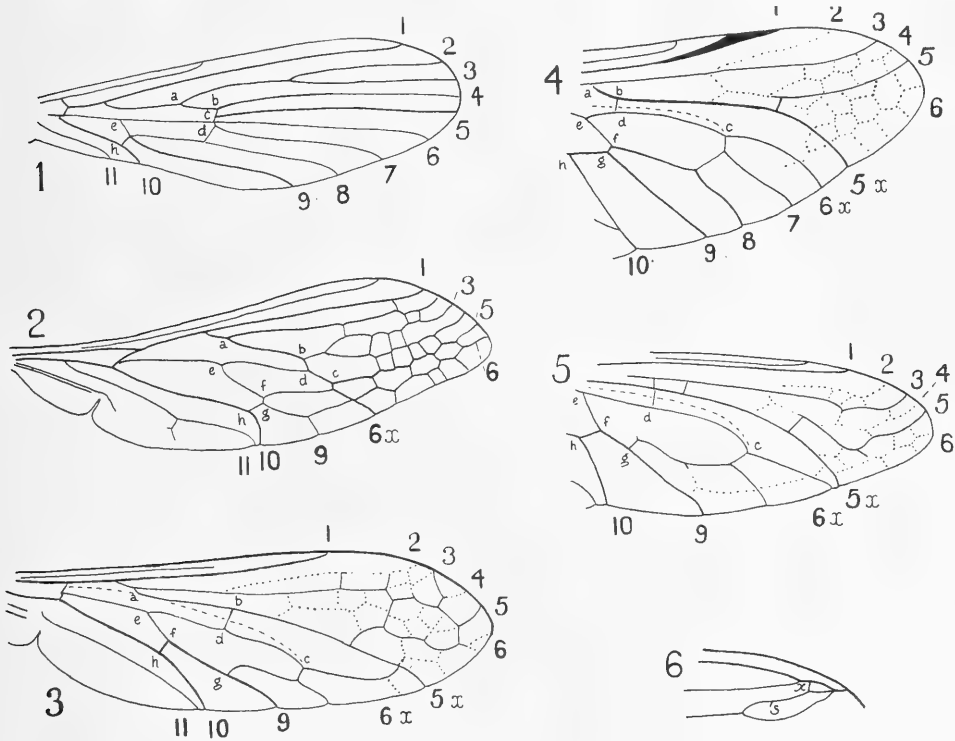
These Nemestrinidae conform to the Comstock notation over the basal half of the wing in a manner that is lost in most other families. Here the arrangement of the veins is alternate convex (+) and concave (-) with one exception, this being the possible true first anal vein (1A), the so-called first anal being a concave vein. This sequence with the Comstock notation is as follows:

+	-	+	-	+	-	+	-	+	-	+
C	Sc	R	R ₂	MA	MP	Cu ₁	Cu ₂	?	1A	2A

Several of these veins branch into the apical half of the wing, beyond those points that Needham refers to as the cord, and there take a pathway left by the disappearance of veinlets out of the original meshwork. It seems that the veinlets disappeared in a somewhat haphazard manner, leaving behind an irregular assortment of apparent branches that do not coincide homologously in the various sections of the Diptera.

For instance, Comstock's vein M_1 (convex) in Tabanidae, cannot be the homologue of the vein M_1 (concave) notated as such in Nemestrinidae and primitive Nematocera, their respective paths having followed different sets of veinlets. Similarly the difference seen in the venation of Mecoptera must have come about in the same manner and the veins bearing the same notation there are not all homologues of primitive Dipterous veins.

The Vein MA.—It has been shown in these "Notes" that the convex *vena spuria* of Syrphidae has its origin in the vein MA. In the more primitive Nematocera (Text-fig. 1) it seems that MA (notated as branch 5) has disappeared basally but continues to the wing apex, becoming there known as vein R_s . The complex part of the *vena spuria*, therefore, does not occur in families like Tanyderidae, Psychodidae and Culicidae, where the so-called R_s is coincident with MA in both character and position.



Text-figures 1-6.

Fig. 1.—Wing of the Psychodid genus *Nemopalpus* showing simple, straight and slightly diverging veins of which those notated 1, 5, 9 and 10 are convex.

Fig. 2.—Wing of the Nemestrinid genus *Megistorhynchus* (after Bequaert, 1935), similarly notated. The veins 1, 5, 6x, 9 and 10 are convex.

Fig. 3.—A reconstruction in dotted lines of *Bombylius namaquensis* Hesse. The veins 1, 5, 5x, 6x, 9 and 10 are convex.

Fig. 4. The venation of *Tabanus lasiophthalmus* Macq., similarly treated.

Fig. 5.—The venation of *Anthrax stellans* Loew., likewise treated showing how the base of vein 4 (concave) runs in continuity with the apex of vein 5 (convex), thus explaining how this complex arose in Tabanidae.

Fig. 6.—Part of the radial field of *Diochlistus neogracilis* new species, showing abnormal characters in a spur marked "s" and a cross-vein marked "x" found on one specimen.

In the reticulate venation of Nemestrinidae (Text-fig. 2), however, MA is less easily detected and runs in continuity with a complex. In Asilidae MA and R_s amalgamate basally and this seems to have happened in *Megistorhynchus* (Text-fig. 2), forming the complex V-S passing through the junction points "a" and "b", beyond which

the vein becomes concave, and hence part of the radial field. If the crossing vein between junction points "b" and "d" happens to be convex, then MA might pass through this to point "c" and thence to the apical wing border. However, the trend in Nemestrinidae is for MA, coincident with V-S, to form the oblique vein ending at point 6x, the whole being convex, except sometimes at its tip, where it may be definitely concave or missing.

Bombyliid Venation.—Text-figure 3 shows the remnant of a reticulation that occurs on *Bombylius namaquensis* Hesse, in which an attempt is made to reconstruct the reticulation by dotted lines. This reconstruction corresponds to veins in Text-figure 2 in many respects. The line of the crease presumed to be the vein V-S is incorporated by a broken line. This figure indicates how the complexity of reticulation may pass a vein of the radial field out of the direct line and back again. It is showing in this instance the third vein interrupted, but through a cross-vein it incorporates a section of the fourth vein, then another cross-vein directs it back to the original course. In this manner the loop in veins is brought about, the loop being a conspicuous feature in various sections of Bombyliidae and extraordinarily pronounced in some Lomatiinae.

Strongly curved veins developed in this way may tend to straighten out to a simple longitudinal vein and become difficult to unravel into its constituent parts in a convincing manner, which difficulty also applies in cases where a vein breaks, leaving a gap unfilled. The capture of the apical part by an adjacent vein in the latter case is now a well-known phenomenon.

Tabanid Venation.—As the Tabanid wing is usually taken to be the standard venation of the lower Brachycera, it is rendered here on the understanding that this arises from a reticulate venation and is shown in Text-figure 4, using *Tabanus lasiophthalmus* Macq., drawn from a photograph by Dr. C. B. Philip.

The vein 1 is slightly out of alignment and vein 2 is absent. Vein 3 is fairly normal, but vein 4 is only retained towards its base, yielding a short appendix to the apparent vein 5, which traverses the area between the original line of veins 4 and 5, and so becomes an apparent attempt to straighten out a complex course. Vein 6 is eliminated.

There seems to be no good example of an intermediate stage to illustrate this development in Tabanidae, but in Bombyliidae the feature is easily traced, as shown in Text-figure 5, based on a photograph, also by Dr. Philip, of *Anthrax stellans* Loew. Here obviously the contours of veins 4 basally and 5 apically run in continuation with a cross-vein between them, vein 5 itself having first become divided by a gap, and the basal part of this is in continuity with a complex of cross-veins of the median field. The apex of the latter is marked 5x.

Remarks.—I am indebted to Dr. C. P. Alexander for the loan of his correspondence with several students of venation, including that of Dr. C. B. Philip, who independently forwarded to me his two manuscripts on the subject. To Mr. H. Audcent I owe the loan of two papers by Vignon and Séguy (1929) and other aids.

In several cases "supernumerary" veins were regarded as a retention of characters from a primitive venation, as viewed by Needham, and the idea that originally the venation was a reticulate one was approached only by Dr. Philip, who did not pursue the subject. However, as many authors are now interested enough to publish these variations in venation not normal to the species, their importance in interpreting venation must be generally felt. In this regard, figures drawn from photographs by Dr. Philip may not be typical of their species, but showing slight variations selected by him.

The views here expressed are not entirely new on this account alone, but the principle as applied here may prove welcome as a method of studying anomalies so plentifully provided in the venation of Diptera and that cannot be accounted for under the Comstock system.

Interpretation of the median field still offers difficulties, and it will be noted that those veins built up with a series of cross-veins, namely those notated 5x and 6x, are convex, though in part are apparently composed with pieces of concave veins as well. Also it must be noted that any of those veins treated here as simple may prove themselves to be complex in origin.

ASILIDÆ.

Genus CYANONEDYS Hermann.

There are three species of this genus of Atomosiini, all described by Hermann (1912), and at about the same time Ricardo (1913) described them under genus *Clariola*. In Australian collections only two of these have been recognized, and in their descriptions there may have been some misunderstanding of specific characters which are not as constant as expected.

Key to species of Cyanonedys.

1. Face and frons golden. Adomen with white pubescence only on the four last segments. (Not seen.) *lugubris* Herm.
Face and frons otherwise coloured. Two basal segments of the abdomen with white hairs 2
2. Abdomen rather long, narrow and uniform in width. Male with black hairs intermixed with the otherwise white moustache *hornii* Herm.
Abdomen broader and shorter and the two basal segments slightly constricted. Moustache entirely white and only occasionally is some black found mixed in it *leucura* Herm.

In the Agricultural Department, Brisbane, one specimen of *C. leucura* is labelled as from the nest of *Pelopaëus* (Sphegidae), having emerged in the office.

OMMATIUS FIMBRIATUS, new name.

Ommatius queenslandi Malloch, 1929, PROC. LINN. SOC. N. S. WALES, 54:409, figs. 4 and 6—*nec Ricardo*, 1913.

Synonymy.—*O. queenslandi* Ric. was based on a male, 9 mm. long, from Stannary Hills, north Queensland, and to it conform Brisbane specimens the terminalia of which were described in 1928 and redrawn in 1935. Between the latter dates Malloch (1929) referred to males with distinctive terminal parts and a length of 14 mm., from Cairns and Gordonvale, and it is for this species that a new name is given here.

Characters.—The smaller species of *Ommatius*, of which this is one, are very much alike, but only three species known have the white moustache, namely *O. dimidiatus* Macq., distinguished by having a distinct subapical ring on the posterior femora and frequently black hairs are included in the moustache; *O. queenslandi* Ric. always with uniformly dark femora; and the present species with red on the basal third of the hind femora, but this may vary. In addition this species has the costa inflated on the male whereas it is simple on the others.

The chief difference is in the form taken by the male terminalia, which differ in the upper forceps, and in the present species the ventral plate has a terminal row of closely packed, elongate bristles (fimbriate), upon which character the name is based. This species is considerably larger than the other two, and it is possible that Ricardo's female specimen, said to be 14 mm. too, may belong here.

Habitat.—Queensland: one male from Realynech, 20th January, 1929, in the Department of Agriculture, Brisbane, which specimen becomes the holotype.

BLEPHAROTES CORIARIUS Wiedemann.

In collections three species of *Blepharotes* have been confused under the name *coriarius*, from which complex Ricardo separated one under *flavus* on its lighter colour of the abdomen. Unfortunately from this point the literature became confusing, as she gave the length of her species as 35 mm., as against 27 mm. for *coriarius* after stating the latter was the bigger.

Dakin and Fordham, drawing attention to the size discrepancy, gave 40 mm. for *coriarius* and 30 to 35 for *flavus*, notwithstanding Wiedemann gave only 15 linien (about 30 mm.) for his original measurement.

The identification of *coriarius* Wiedemann must rest upon the fact that the last two lateral tufts of the abdomen are recorded as being white by Wiedemann, and this corresponds to figures given in the *Australian Encyclopedia*, 1925, plate XI, fig. 37, and again in Tillyard's *Insects of Australia and New Zealand*, 1926, plate 20, fig. 24. As

this character occurs only on the male and specimens are showing wide discrepancies in other colour characters, there appears to be no reliable feature for distinguishing females.

The third species is readily distinguished on the colour of the thorax and the spots there are usually distinguishable even on rubbed specimens; moreover, this form, *punctatus* Hardy, differs considerably in the antennal proportions. On *coriarius*, given the smallest antennal segment as being one unit, the formula for consecutive segments is 7:5:27:1:6 for the male and 7:5:30:1:7 for the female, making the style (fourth and fifth segments combined) only one-quarter the length of the third segment. Whereas this agrees with the proportions on *flavus*, it considerably differs from that on *punctatus*, where the style is about as long as the third segment.

Figures of the terminalia were given in Hardy, 1921, p. 276, but it must be noted that the names there attached to figures 9 and 10 were inadvertently interchanged—figure 9 should have been *flavus* (syn. *brisbanensis*) and figure 10 *punctatus*.

Key to species of the B. coriarius-group.

1. Antennal arista only one-quarter the length of the third segment. Thorax without markings. 2
 Antennal arista about as long as the third segment. Thorax with conspicuous spots. Male
 terminalia conforming to that in Hardy, 1921, fig. 10 *punctatus* Hardy
2. Larger average size and normally darker abdomen. On male the two last tufts of lateral
 hairs are entirely white or almost so, and the terminalia have a process on the lower
 forceps corresponding to that in Hardy, 1921, fig. 11 *coriarius* Wied.
 Smaller average size and normally the abdomen is lighter coloured. On the male the last
 two tufts of lateral hairs are entirely black or almost so, and the terminalia are without
 the process, conforming to that in Hardy, 1921, fig. 9 *flavus* Ric.

MYDAIDAE.

DIOCHLISTUS NEOGRACILIS, n. sp.

Male.

Face black with abundant bright golden-yellow hairs extending to summit along the eye margins, and the hair on the summit is similar, but the colour appears brownish till seen by reflected light. Rear of head with some silvery-grey pulverulent overlay along the eye margins.

Thorax with three black shining stripes on a dull ground and not reaching scutellum, which, like the humeral callus and lateral border, is yellow-brown. Metapleura strongly tubercle-form.

Abdomen conspicuously clubbed with the whole first segment and the lateral and posterior margins, together with traces on the anterior margin, of the second, third and fourth segments black. Elsewhere on these three segments yellow-brown both dorsally and ventrally. Fifth segment to apex wholly black with yellowish pubescence on dorsal and some on ventral area.

Legs yellow with parts black, including the swollen part of the posterior femora, corresponding with *gracilis*. Wings infuscated on costal and radial areas, fading beyond to a hyaline posterior margin. The veins R_1 and R_5 are petiolate on most specimens, conforming to *aureipennis*, but the character varies with most females and a few males. An aberrant case is a specimen with a spur on R_4 showing equally on both wings, and a cross-vein on one wing, as illustrated.

Female.

This differs from the male in the abdominal pattern and shape, being longer and cylindrical. The areas of yellow-brown extend from the second segment to the apex, thus making the abdomen banded dorsally with yellow and black, but ventrally the yellow occurs only on the second segment and traces of it varying in amount on the third; elsewhere black.

The length is very variable, averaging about that of *gracilis*, almost to that of *aureipennis*, which is much larger in actual bulk.

Habitat.—Queensland: Stanthorpe, 10–18 November, 1927. There are nine males and three females, eight of which bear on the label "H. Jarvis", and four are unlabelled.

Remarks.—This species runs to *gracilis* in Mackerras' (1928) key but differs from that species remarkably in the abdominal markings, the female especially so, being strongly banded black and yellow in a way that forms an intermediate stage leading to *aureipennis*, with which most of the specimens agree in the petiolate cell of the radial field, a character unknown outside these three species, even as an aberrant character.

With this species the two early proposed genera *triclonus* Gerstaecker, 1868, and *Harmophana* Thomson, 1869 (see key in Hardy, 1942, p. 201) are united to make a group of closely related species separated in the following key.

Key to the gracilis-group (Triclonus).

Yellow and black species in which the antennae are elongate.

1. Abdomen largely yellow, the black bands being highly reduced. Wings yellow *aureipennis* Westw.
Abdomen either strongly banded black and yellow, or largely black. Wings infuscated black-brown 2
2. Female with abdomen banded black and yellow beyond the first segment. Male with only the second to fourth segments so banded. Face black *neogracilis*, n. sp.
Yellow of abdomen reduced to a pair of spots on second to fourth segments 3
3. Face black. Legs strongly marked with black *gracilis* Macq.
Face yellow. Legs light coloured *melleipennis* Westw.

HERMETIA ILLUCENS L.

H. pallidipes Hill, 1919, PROC. LINN. SOC. N. S. WALES, 44: 454.

Synonymy.—The description of *H. pallidipes* given by Hill is covered by colour variations of the introduced *H. illucens* L. found in Brisbane gardens, and in addition the figures given by Hill agree. As the genus is American and quite distinct from the indigenous genera of Australia, there had long been doubt concerning the generic status of the presumed Australian species. The synonymy throws light upon the introduction into Australia.

History.—This fly was brought into Queensland by the Commonwealth Prickly Pear Board, and not long afterwards specimens were collected in northern New South Wales. During recent years it has become a garden fly in Brisbane. It has also been found in orchards around Sydney, in which city it was reared from vinegar vats, which suggests that it might become a minor pest of industry.

The handling of consignments from America by the staff of the Board was not conducive to the breeding of this fly under the artificial conditions used, but the ten importations in rotting vegetation between May, 1921, and April, 1923, may have allowed ample escape over the period. Whether this be so or not, the above synonymy suggests that the fly was already in this continent five years before the Board had been formed. The two specimens described by Hill were collected on garden plants at Darwin in February, 1915.

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THE DIPTERA OF THE TERRITORY OF NEW GUINEA. XIV.*

FAMILY TABANIDAE. PART III. TABANINAE.

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(Seventy-one Text-figures.)

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INTRODUCTION.

This part concludes the review of the Tabanidae of New Guinea, begun by the late Mr. F. H. Taylor in these PROCEEDINGS (1946) and continued by me (1947). In addition to the material detailed in my previous paper, I have had small collections lent for study by Dr. J. Bequaert of Harvard, Mr. D. J. Lee of Sydney, N.S.W., and by the South Australian Museum, to all of whom I am most grateful for this co-operation. Dr. Max Beier, of the Naturhistorisches Museum, Vienna, very kindly allowed me to borrow the types of *T. furunculigenus* Dol. and *T. cinnamoneus* Dol., both of which had been described later under different names.

In the previous part of this paper I made one or two errors in location of type specimens. The following are in the Museum of Natura Artis Magistra, Amsterdam, and not in the Rijksmuseum of Natural History, Leyden, as stated: *Pareucompsa femoralis* Ric.; *Lilaea de meijerei* Ric.; *Lilaea vittata* Ric.; *Scaptia novaeguineensis* Ric.

The exact positions of the various camps of the Archbold Expedition were given in my previous paper. Those of the Lorentz Expedition of 1909-10—Bivak Island, etc.—are in the general region of the Lorentz River in S.W. New Guinea, about 05°S., 138-139°E. One locality where Mr. W. Stüber collected is given on labels as "Hollandia, 140°E., 3°10'S."; this is a place about 60 miles S.W. of Hollandia, near the headwaters of the Idenburg River, at about 1,500 ft.

With the exception of *T. yulensis* v. Röder, and three species described by Doleschall, all the known species of Tabaninae are described and figured in Schuurmans Stekhoven's valuable work on the Tabanidae of the Dutch East Indian Archipelago, but they are scattered among the oriental species, and the grouping is not one that I can

* Continued from these PROCEEDINGS, lxxii, 1947, 142.

follow. Since I have re-grouped the species I have also re-described them, very briefly, where I have material available. Certain points are omitted from the descriptions where there is uniformity throughout—e.g., the proboscis is not mentioned where it is moderately short, with fleshy labella occupying about half the total length; and if the coxae are not described, they should be assumed to agree with the adjoining pleura in tomentum and colour.

There is very much variation in details of coloration, and the proportions of frons and callus are relied upon as final arbiter in deciding between two different species. For this reason, and because secondary sexual differences often make it difficult to associate males and females with certainty, I have given little attention to males. The figures quoted as "frons proportions" are the readings of a micrometer eyepiece between the eyes at the vertex, at the antennal angles, and the length of the frons from vertex to antennal angles. The frons is said to diverge if it becomes broader towards the antennae, and to converge if it narrows towards the antennae. "Index" is length of frons divided by breadth at antennal angles.

I have again used some generic names from Enderlein's "Neues Tabanidensystem" of 1922, 1925. These groupings have been adversely criticized because the keys make use of variable characters, particularly of the venation, but it is becoming clear that many of Enderlein's group-concepts have a real basis. The difficulty is to re-define them on more constant characters.

SUBFAMILY TABANINAE.

The classification of this, much the larger, subfamily is chaotic. In every region there are one or two isolated species for which a genus can, with confidence, be erected, and there are many groups of species that can be recognized in collections by their general appearance and pattern. When one tries to find key-characters to separate these groups there are so many intermediates that authors usually end by dumping most of the species into the genus 'Tabanus'. Groups of species are then defined within this complex.

Schuermans Stekhoven (1926)* uses the colour and pattern of the abdomen as his main group-character. This has to be done eventually, but it is better to use structural characters as far as they will go. In recent years Philip and other North American workers have made use of the basicosta, or *subepaulet* (Text-fig. 1). In the New Guinea species this gives a convenient, apparently sound division. Nearly all those with a hairy subepaulet have a very narrow frons, tapering towards the antennae; these are the most 'Tabanus-like' forms, and are here referred to the genus *Tabanus*. This element seems to be most nearly allied to the genotype, the European *T. bovinus* L., which also has hairy subepaulets, though a somewhat broader frons.

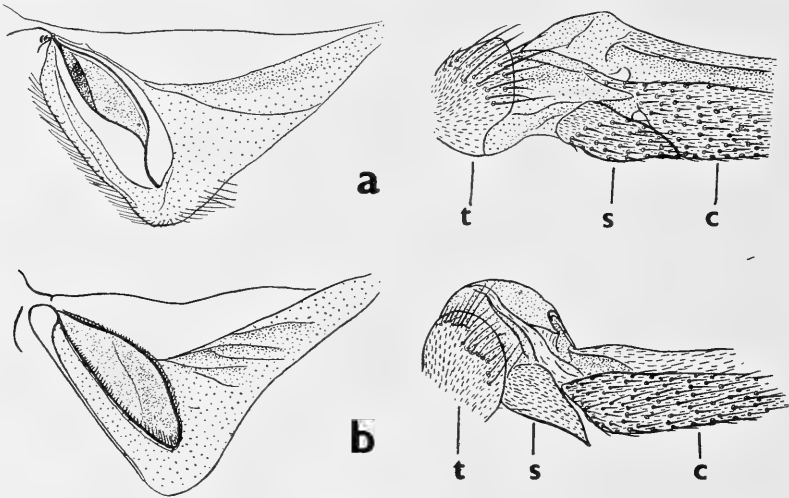
The New Guinea Tabaninae with bare subepaulets are more diverse in form, but nearly all have a broader and less tapering frons. Besides several distinctive genera, such as *Neobolbodimyia*, there are a number of species-groups of distinctive appearance. A number of very small forms are, I believe, peculiar to the New Guinea fauna, and have been separated off by Enderlein as his subfamily Chasmiinae, containing two genera, *Chasmia* and *Chasmiella*. While it is difficult to separate off this group on any one character, in the aggregate of a number of small points it seems distinctive, and the two genera are here accepted. Two species—*fasciata* and *parvicallusa*, n. spp.—are rather anomalous. I have included them in the genus *Chasmiella*, but they differ markedly from the other species. In some ways they are intermediate between *Chasmiella* and *Chalybosoma*, g.n.

* It should be noted that Stekhoven uses the term 'Pteropleuron' for the callus which lies immediately before the transverse suture on each side of the thorax, and which is very prominent in Tabanidae. This should properly be called the *notopleural* callus, or lobe, and the term pteropleuron applied to the pleural sclerite immediately below the wing-base. This is a point to beware of in using Stekhoven's descriptions.

The remaining groups of species with bare sub-epaulets are retained in one genus though eventually some of them—e.g., the yellow, patternless forms centring round *T. sol* S.S.—will probably have to be referred to genera which are present in adjoining regions. Since the genotype of Taylor's genus *Cydistomyia* comes in this section I have used this as the generic name, while fully realizing that this grouping brings together many diverse elements, and that the genotype itself is rather an isolated species.

Mr. G. H. Hardy was good enough to send me a synopsis of his forthcoming paper on Australian *Tabanus*, in which he uses the name *Cydistomyia* for a subgenus. He uses the frontal index as a primary character, and draws his dividing line in a different place from mine, so that he includes *Cydistomyia* in the forms with a narrow frons (i.e., my genus *Tabanus*), and reserves the name *Tabanus* for a few species with two separate frontal calli. I hesitate to quote from his unpublished work, and do so merely to point out that his '*Cydistomyia*' may not cover the same group of species as mine.

A character often associated with the hairy subepaulet is the possession of a pair of prominent lips to the thoracic spiracles (Text-fig. 1), while in most species with bare subepaulet the spiracle does not protrude outside the pleural wall. This association is



Text-figure 1.

Prothoracic spiracle and base of wing: *a*, *Tabanus angustilineatus*, n. sp.; *b*, *Cydistomyia atuensis*, n. sp., showing t = tegula; s = subepaulet; c = costal vein.

not invariable, and the appearance may sometimes be altered during the process of drying, but there seems to be a strong correlation. I have seen many species from other regions which follow the same rule, though there are notable exceptions, in the Palaearctic Region. Certain Mediterranean species, such as *T. apricus* Mg., and *T. graecus* Fabr. have a bare subepaulet and a spiracle with lips.

In a recent paper Hassan (1944), *Trans. R. ent. Soc. Lond.*, 94, 103-153, has described two forms of spiracle-regulating mechanism which resemble these. He associates the lipped (or external) type with a humid environment, and the lipless (or internal) type with drought. It would be interesting if the habitats of these Tabanidae showed such a correlation.

DISTRIBUTION.

Unlike the Pangoniinae, the Tabaninae in the collections before me do not show any marked features of distribution. There are one or two coastal species (*T. rufinotatus* Big., *Cydistomyia caesius* Wlk., perhaps *Chasmiella papouinus* Wlk.) and a few have spread into New Guinea from other regions. *T. ceylonicus* Schin. extends from Ceylon south-eastwards, and is nearing the end of its range in New Guinea. The smaller

Cydistomyia, immigrans, inopinata, misimensis, n. spp., seem to be a spread into Papua of Australian elements. The *cohaerens*-group of *Tabanus* also extends into Australasia, and, in New Guinea, seems to occur mainly at the lower altitudes. Beyond this, the distribution of species seems to be an individual matter, and, as at present known, is largely an accident of collecting.

KEY TO GENERA OF TABANINAE OCCURRING IN NEW GUINEA.

Hind tibiae without spurs; ocelli sometimes present, more often vestigial or absent.

(Genera in italics have not been seen by me; those in square brackets are not yet known from New Guinea.)

1. Subepaulet (basicosta) with bristly hairs as well-developed as those on the costal vein (Text-fig. 1a). Thoracic spiracles, especially the anterior ones, generally with prominent lips, which protrude above the general level of the pleura (Text-fig. 1a). Frons very narrow (index 5-10), tapering towards antennae *Tabanus* Linn.
- Subepaulet (basicosta) with a velvety pubescence, but without bristly hairs, thereby contrasting in appearance with costal vein (Text-fig. 1b). Thoracic spiracles generally protruding little or not at all above the level of pleura, without prominent lips (Text-fig. 1b). Frons usually—but not invariably—broader and not so tapering 2
2. Labella of proboscis short, not more than one-third of total length of proboscis. Anal cell usually open, or barely closed. Median ocellus present, some distance before vertex, which is generally deeply grooved. Antennae usually more or less elongate, first segment rather longer than broad, third segment 3-4 times as long as broad, with a less conspicuous tooth. Vein R_4 making an acute angle with R_5 . Small, delicate species. 6-9 mm. (Enderlein's subfamily Chasmiinae) 3
- Labella nearly always larger, at least half total length of proboscis.* Anal cell definitely closed, apical portion of vein Cu_1 slightly convex. Median ocellus sometimes present, usually absent, and vertex not grooved. Antennae of varying structure. Vein R_4 often right-angled at its base, sometimes with an appendix. Species generally larger, more robust 4
3. First antennal segment twice as long as it is thick, cylindrical in side-view. Third antennal segment parallel-sided, tooth insignificant *Chasmia* End.
- First antennal segment not twice as long as thick, in side-view triangular, as in *Tabanus*. Third segment with a more or less distinct tooth *Chasmiella* End.
4. Thorax and abdomen partly metallic blue-green, with or without pale areas. Subcallus and central area of face bare and shining. Tibiae bicoloured, white basally, black apically, but not appreciably flattened *Chalybosoma* gen. nov.
- Body not metallic 5
5. First antennal segment slender, subcylindrical in side-view, longer than broad, often much longer (tribe Diachlorini) 6
- First antennal segment subtriangular in side-view, not much longer than broad 7
6. Subcallus swollen, shining [*Udenocera* Ric.]
- Subcallus not swollen, nor shining, though frons and callus may be shining [*Paracanthocera* End.]
7. Third antennal segment without a trace of a tooth. Ocelli present in a large, equilateral triangle *Ommia* End.
- Third antennal segment with the usual tooth 8
8. Subcallus swollen, shining 9
- Subcallus not swollen and shining† *Cydistomyia* Taylor
9. First antennal segment greatly inflated, shining *Neobolbodimyia* Ric.
- First antennal segment somewhat swollen, but not shining 10
10. A distinct ocellar callus present, but no ocelli. Face swollen, bare and shining. Second antennal segment with a dorsal lobe *Japenoides* gen. nov.
- No ocellar callus. Face tomented. Second antennal segment without a dorsal lobe [*Neotabanus* Ric.]

Key to the New Guinea Species of *Tabanus*.

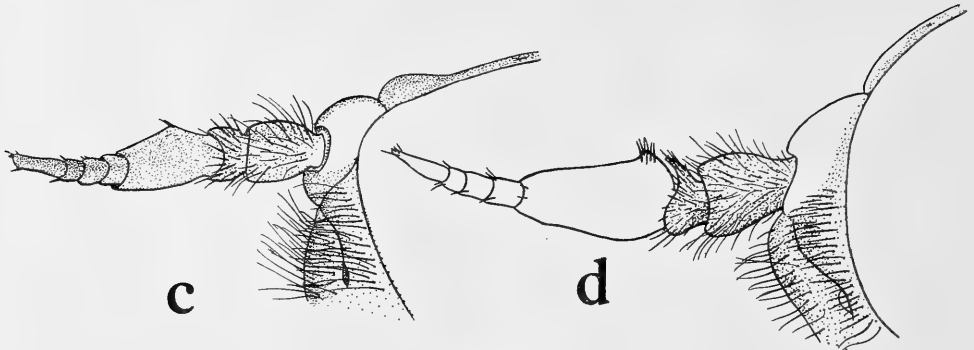
1. Subcallus swollen, bare and shining. Front tibiae broad, flattened, and conspicuously white on basal half *ceylonicus* Schin.
- Subcallus covered with tomentum, not markedly swollen 2
2. Third antennal segment with a forwardly-directed dorsal process (Text-figs. 5, 28). Frontal index 9-10, frons converging, callus almost linear. Large species, over 18 mm. 3
- Third antennal segment without such a well-developed process, though a distinct tooth may be present 4

* In dried specimens the labella sometimes become impaled on the tips of the stylets, and the stem of the labium is stretched, making it seem unusually long and attenuated.

† In *Cydistomyia imitans*, n. sp., the subcallus is bare, but is not developed as a prominent structure, and is not divided from the parafacials by a well-developed suture (see Text-fig. 2).

3. Large yellow and dark brown species, with banded abdomen. Wings brownish on apical half, yellowed towards base *aurivittatus* Ric.
 Large, dark mahogany species, abdomen shining, without pattern, and with uniformly black hairs, except for conspicuous orange tufts laterally on segments 5 and 6, and a few orange hairs at extreme apex. Wings deeply browned along veins *denticulatus* Ric.
4. Abdomen without median triangles or spots 5
 Abdomen with median triangles or spots. This includes species in which triangles of pale hairs can be seen, even if the tergite itself is uniformly coloured 17
5. Abdomen predominantly yellow or orange *cinnamomeus* Dol.
 Abdomen predominantly dark brown or black 6
6. Vein R_4 with appendix. Antennae, palpi and abdomen, dorsally and ventrally, and legs—black. Mesonotum strikingly contrasted in colour with abdomen. (Rubbed specimens of *productus*, n. sp. may run down to this point, but mesonotum is not strongly contrasted with abdomen, and third antennal segment is broad and strongly toothed) .. 7
 Vein R_4 without appendix; or antennae, palpi and abdomen not black; or mesonotum not strikingly contrasted with abdomen 9
7. Mesonotum thickly grey-dusted *stuberi*, n. sp.
 Mesonotum shining orange-red 8
8. Beard and fore-coxae brown-haired *illustris* Ric.
 Beard and fore-coxae white-haired *flammeus* S.S.
9. Mesonotum heavily tomented, grey or greenish, contrasting sharply with black abdomen .. 10
 Mesonotum not strongly contrasting with abdomen 11
10. Third antennal segment black. Mesonotum greenish, with short black hairs. First posterior cell distinctly narrowed towards wing margin *wollastoni* Ric.
 Third antennal segment orange. Mesonotum greyish with mixed pale and black hairs. First posterior cell not strongly narrowed towards wing margin *doreicus* Wlk.
11. Wings rusty-yellow, contrasting strongly with thorax, abdomen and legs, all of which are black with black hairs *flavipennis* Ric.
 Wings browned, but not rusty-yellow, not in marked contrast with a black body and legs 12
12. Larger species (18 mm. or more). Wings browned, with clearer areas in many cells, but not noticeably paler at wingtip. Third antennal segment obscurely reddish, not contrasting strongly with rest of antennae 13
 Smaller species (16 mm. or less). Wings may be browned at base, with tip distinctly paler, or may have colour just along veins. Third antennal segment orange, in contrast with first two segments, which are brownish 14
13. Pleura with dark brown hairs. Third antennal segment dull orange *pollinosus* Ric.
 Pleura reddish brown, with reddish brown hairs. Third antennal segment bright orange *angusticallosus* S.S.
14. R_4 with appendix. A blue-grey species with darkened wings. Frons very tapering (Text-fig. 34) *opalescens* S.S.
 R_4 without appendix. Not a blue-grey species, frons not so tapering 15
15. Black-brown species. Hairs of prothorax and squamal fringe black. Brown colour of wing-tip spread evenly along veins, no distinct clouds *furunculigenus* Dol.
 Hairs of prothorax and squamal fringe pale. Brown colour of wing stronger along veins, and forming distinct clouds on crossveins and on fork of R_4 16
16. Bluish black species, with a bluish sheen on some, at least, of the abdominal tergites. Palpi bluish with bluish sheen *recusans* Wlk.
 Brown species, with abdomen and venter yellowish. No bluish sheen. Palpi white, with black hairs *vanleeuweni*, n. sp.
17. A middle-sized (12-18 mm.) grey species, with three rows of pale triangles on abdomen, merging into three almost parallel-sided stripes. Callus sometimes broken into two *rufinotatus* Big.
 Without three distinct rows of pale triangles 18
18. Third antennal segment exceptionally broad and short (Text-figs. 35, 39) 19
 Third antennal segment not broad and short 21
19. R_4 with long appendix. A middle-sized species, black, with only a few white hairs in middle of each segment *productus*, n. sp.
 R_4 without appendix. Abdominal triangles distinct 20
20. Larger (15 mm.) species, dark brown, shining, with distinct small, pale median triangles. Callus rectangular, with a linear extension (Text-fig. 35). Palpi normal *lenticulatus*, n. sp.
 Smaller (12 mm.) species, with greyish thorax and reddish brown abdomen, on which triangles are distinct, yellowish. Palpi short, plump and pointed. Callus (Text-fig. 39) *truncatus*, n. sp.

21. Middle-sized (15 mm.), grey and black species, with one median row of very distinct, separated pale spots on the abdomen. Thorax with two distinct grey stripes. Frons relatively broad, index 6 or less (*semicircularis*-group) 22
 Either larger, or brown, or—if middle-sized and grey—then without a median row of very distinct, separated pale spots on abdomen. Frons relatively narrow, index $6\frac{1}{2}$ -10 .. 24
22. Third antennal segment and following segments relatively elongate (Text-fig. 12). Wings clear, without clouds or spots on crossveins, and with small appendix. Abdominal median spots triangular, diminishing in size from second segment backwards. Frontal callus as in Text-figure 12 *exagens* Wlk.
 Third antennal segment and following segments relatively shortened (Text-figs. 17, 44). Wings with distinct brown clouds, especially on radial fork and at apex of discal cell. Abdominal median spots rounded in outline 23
23. Frontal callus elongate (Text-fig. 17). Subcallus with uniformly yellowish tomentum. Shorter and broader species, in which the first abdominal spot is usually isolated and the rest bunched together. Generally with distinct appendix to R_4 .. *semicircularis* Ric.
 Frontal callus short, with fine linear extension (Text-fig. 44). Subcallus, around antennal sockets, dark velvety brown. More elongate species, in which the abdominal median spots are evenly spaced. Generally without appendix to R_4 *angustilineatus*, n. sp.
24. Relatively small species (12-14 mm.), in which the median spots, if present, tend to merge into a parallel-sided stripe. Fore-tibiae distinctly paler on basal half (*cohaerens*-group) 25
 Mostly relatively larger species (16 mm. upwards). Median spots not tending to merge into a median stripe. Fore tibiae only indistinctly paler at base, or uniformly coloured 27
25. Mesonotum without, or with only inconspicuously golden scaly hairs among the black hairs. First antennal segment relatively longer (Text-fig. 11) *divisus* Ric.
 Mesonotum with conspicuous recumbent golden scaly hairs among the black hairs. First antennal segment relatively shorter and broader (Text-figs. 10, 42) 26
26. Frons broader, more parallel-sided, index 8 (Text-fig. 10). Lighter-coloured species, with yellowish abdomen and grey thorax. Median abdominal stripe pale and distinct *cohaerens* Wlk.
 Frons more tapering, index 10, narrowest just above antennae (Text-fig. 42). Darker species, abdomen brown or reddish brown. Median abdominal stripe indistinct *approximatus*, n. sp.
27. Female with third antennal segment and fore-femora black 28
 Female with third antennal segment and fore femora either orange or obscurely darkened, not black 31
28. Frons almost parallel-sided, index $6\frac{1}{2}$, callus flask-shaped, with broad extension (Text-fig. 41). Vein R_4 without appendix *infuscatus*, n. sp.
 Frons tapering towards antennae. Vein R_4 with appendix 29
29. Abdomen shining dark brown, with clear-cut median triangles. Callus short, rectangular, with fine linear extension (Text-fig. 40) *patriarchus*, n. sp.
 Abdomen black, with a bluish sheen in certain lights, triangles of pale hair very indistinct 30
30. Frons strongly tapered, index $10\frac{1}{2}$ (Text-fig. 34). Abdomen rather narrow .. *opalescens* S.S.
 Frons not so strongly tapered, index $7\frac{1}{2}$ (Text-fig. 39). Abdomen broader, species of normally stout appearance *truncatus*, n. sp.
31. Parafacial hairs and beard brown. Frons relatively broad, more parallel-sided. Callus clearly divided into a broad basal part and a linear extension. Third antennal segment narrower (Text-figs. 13, 14) 32
 Parafacial hairs white or yellowish. Frons relatively narrow, or more tapering, or callus tapering smoothly, without a distinct neck. Third antennal segment broader (Text-figs. 15, 43) 33
32. Callus shorter, with long linear extension reaching nearly to vertex. Third antennal segment less slender (Text-fig. 14) *indistinctus* Big.
 Callus basally broad and large, with stout median extension reaching only half-way to vertex. Third antennal segment slender, tooth small (Text-fig. 13) .. *rubriventris* Macq.
33. A larger, more reddish species. Abdomen (fresh specimens) clear reddish brown, covered with fine black hairs, and with distinct triangles. When rubbed, almost uniformly brick-red. Wings strongly stained brown. Femora, especially hind femora, with predominantly black hairs. Third antennal segment twice as long as succeeding segments together (Text-fig. 15). Palpi normal *serus* Wlk.
 A smaller, more brownish species, abdomen dark brown, with distinct triangles. Wings very heavily stained brown. Femora, especially hind femora, with predominantly white hairs. Third antennal segment not more than $1\frac{1}{2}$ times as long as the succeeding segments together (Text-fig. 43). Palpi slender, scarcely swollen at base *daruensis*, n. sp.



Text-figure 2.

Antenna and subcallus of: *c*, *Neotabanus ceylonicus* Ric.; *d*, *Cydistomyia imitans*, n. sp.

Genus TABANUS.

TABANUS AURIVITTATUS.

Tabanus aurivittatus Ricardo, 1913, Nova Guinea, ix, zool. 3, p. 394; Stekhoven, 1926, Treubia, vi, suppl., p. 268.

A large, dark brown species, with yellow-banded abdomen and yellowed wings. The frons is long and narrow, with a long linear callus. Third antennal segment bears a prominent forward-projecting process (Text-fig. 5).

♀. *Head*. Frons long and narrow, proportions 18:12:125. Index $10\frac{1}{2}$. Converging towards antennae. Callus almost linear, occupying three-quarters of length of frons (Text-fig. 5). Frons with yellow tomentum and brown hair. Subcallus not prominent, covered with uniform yellow tomentum, without hair. Face similar, facial swelling and parafacials with yellow or brown hairs, beard yellow. Antennae orange, first two segments darker, with mainly black hairs, third segment clear orange, with a strong projection (Text-fig. 5), following segments concolorous. Palpi orange, with mainly orange and a few black hairs. Proboscis yellow basally, black apically, labella about half total length.

Thorax. Mesonotum dark brown in ground colour, heavily covered with yellowish-brown tomentum, without stripes. Hairs mainly black on dorsum, lateral tufts golden except for a tuft of strong black hairs on prealar callus. Pleura with yellow tomentum and yellow hairs. Squamal fringe yellow.

Abdomen. Dorsum dark brown, with broad marginal yellow bands almost half width of segment, and expanded into median triangles which nearly reach the fore border. Hairs black on brown areas, yellow on yellow areas. Venter similar, without median triangles.

Legs. Coxae like pleura. Legs otherwise orange, hind tibiae and tarsi darker. Pubescence mainly golden, with a few black hairs. Hind tibiae with a very conspicuous fringe of golden hairs.

Wings. Membrane stained yellow, especially on fore border and along veins. Vein R_4 angled, but without appendix. Tegula with yellow tuft, subepaulet reddish brown with black hairs like those on costal vein.

Length of body: 24 mm.; *of wing*, 21 mm.

♂. Very closely similar. Eyes with large upper and small lower facets, sharply divided.

Holotype, from Regeu Is. (Lorentz), is in *Natura Artis Magistra*, Amsterdam.

In the British Museum is a paratype from Bivak Island (Lorentz), and there are two females from German New Guinea, Sattelberg, Huon Gulf (Biro). Ricardo and Stekhoven record other specimens from the same localities. The Archbold Expedition took one female at Bernhard Camp, 50 m., 15.x.1938 (J. Olthof), and one male at

Araucaria Camp, 800 m., 20.iii.39 (Toxopeus). In the material on loan from Sydney are two females from Wareo, Finsch Haven (Rev. L. Wagner), and one female from N. New Guinea, Motorbivak (v. Leeuwen).

TABANUS DENTICULATUS.

Tabanus denticulatus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 397; Stekhoven, 1926, *Treubia*, vi, suppl., p. 490.

A large, shining, dark reddish brown species, distinguished by the long tooth to the third antennal segment, and by the conspicuous orange lateral tufts on the fifth and sixth abdominal segments.

♀. *Head*. Frons long and narrow, proportions 18:14:97, index 7, converging slightly towards antennae. Callus linear, slightly expanded at lower end (Text-fig. 28), shining mahogany-brown. Frons with greyish tomentum and black hairs. Subcallus reddish in ground-colour, with thick yellowish tomentum and no hairs. Tomentum of face and parafacials more greyish, hairs black. Beard black. Antennae orange, first two segments darker, with black hairs, third segment bright orange with a very prominent dorsal projection (Text-fig. 28), following segments concolorous. Palpi orange with black hairs.

Thorax. Mesonotum and pleura dark red-brown, rather shining, with sparse greyish tomentum and black hairs. Pre-alar and post-alar tufts and squamal fringe yellow.

Abdomen. Like mesonotum, but more shining. Hairs black, with a black lateral tuft on each segment except the fifth and sixth, which have conspicuous orange lateral tufts. Venter similar.

Legs. Reddish brown with black hairs, coxae similar.

Wings. Membrane yellow, more heavily so basally, up to forks of R and M, clearer areas in base of cell R_1 and centre of cell R_{2+3} .

Length of body, 19 mm.; *of wing*, 19 mm.

♂. Similar.

Holotype, from Hellwig Mts., is in *Natura Artis Magistra*, Leyden.

Described from Hellwig and Wichman Mts., and recorded by Stekhoven from Lorentz's collecting area, Doorman Path, and from S. New Guinea. In the British Museum are three paratypes, and also the following specimens: Papua, Mt. Tafa, 8,500 ft., iii.1934 (Miss Cheesman), two females; Kaindu, Edie Creek, 6,550-7,000 ft. (F. H. Taylor), one female; Weyland Range, 6,000 ft. (O. S. Wickwar), one female.

The Archbold Expedition took a series of specimens at the following localities: Moss Forest Camp, 8,000 ft., x.1938 (Toxopeus), 60 females, one male; Iebele Camp, 6,750 ft., x.1938 (Toxopeus), three females, one male; Lake Habbema, 9,000 ft., viii.1938 (Toxopeus), two females.

In the Sydney Museum Collection from Kaindu, Edie Creek, 6,550-7,000 ft. (F. H. Taylor), three females; Komba (Rev. L. Wagner), one female; Papua, Waria R., 21.2.36 (H. O. C. Littlejohn), one female.

In the Harvard material from Morobe Dt., Mt. Misim (Stevens), one female.

TABANUS POLLINOSUS.

Tabanus pollinosus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 395; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 494.

Concisely described by Miss Ricardo as "A large, black species, the abdomen with a greyish plum-like bloom, thorax brownish. Antennae red, legs black. Wings brown". This description separates *pollinosus* from any other New Guinea species of *Tabanus*, except from *T. angusticallosus* S.S., which was erected for a specimen named as *pollinosus* by Miss Ricardo (see below).

♀. *Head*. Frons very long and narrow, proportions 10:10:92, index 9.2; narrowest in middle (seven units). Callus almost linear. Tomentum of frons, subcallus and face brown, parafacial hairs and beard dark brown. Antennae orange, first two segments darker, with black hairs; third segment brighter, with prominent tooth, but not a long process (Text-fig. 9), following segments slightly darker. Palpi brownish, with black hairs.

Thorax. Mesonotum and pleura brick-red when rubbed, normally obscured by brown and grey tomentum. Fine hairs on dorsum black, with a few reddish brown silky hairs among them. Supra-alar and postalar tufts, and squamal fringe, pale reddish brown.

Abdomen. Large and square, dark purple, covered with a plum-like bloom; this bloom is thicker on first two segments and thins behind, leaving the dorsum dully shining. Hairs all black, without paler median triangles. Venter similar, duller.

Legs. Femora and tarsi black, tibiae very obscurely dark mahogany-red. Hairs black.

Wings. Heavily browned, paler in centres of cells. Tegula with creamy hair-tuft.

Length. Body 18–22 mm.; wing 20 mm.

Described from Simbang, near Finsch Harbour. Type in Dr. Kertesz's collection, and one paratype in the British Museum.

In the British Museum are also six females from Waria R., "series collected both on Papua and New Guinea sides of river", 1935 (Littlechild). In the Sydney School of Public Health and Tropical Medicine are six females from the same locality; one female, Papua, Vailata R., Oct., 1923 (Murray); N.E. Papua, Mt. Lamington, 1,300–1,500 ft. (McNamara). In Mr. Lee's material from New Guinea, Lae, 1947 (Bayley). In the U.S. National Museum Collection from Nadzab, Markham R. valley, Sept., 1944 (Krombein).

TABANUS ANGUSTICALLOSUS.

Tabanus angusticallosus Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 495.

This is very closely similar to *pollinosus* Ric. and may possibly be a form of it. I do not follow all the differences listed by Stekhoven, whose unique type specimen had previously been labelled as *pollinosus* by Miss Ricardo. Yet it seems that two species can be recognized here, a darker and a more reddish brown one, distinguished most easily by the colour of the pleural hairs. These are dark brown in *pollinosus*, red-brown in *angusticallosus*.

Type in the British Museum, from Milne Bay. Also in the British Museum are eight females, Papua, Kokoda, 1,200 ft., ix–x.1933 (Miss Cheesman). In the Harvard collection, one female, Milne Bay, July (R. S. Wind). In Mr. Lee's material, one female, Milne Bay, Feb., 1943 (Mackerras).

A distribution-map of these two forms (Text-fig. 3M) indicates that they are localized in the S.E. of the island as two species or subspecies, *pollinosus* to the north and *angusticallosus* to the south, meeting in the Kokoda-Buna area. Neither species was taken by the Archbold Expedition in the central mountains.

TABANUS WOLLASTONI.

Tabanus wollastoni Ricardo, 1913, *Nova Guinea*, ix, zool., 3, p. 395 (*lapsus*).

Tabanus wollastoni Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 493.

A large species, easily recognized by the greenish yellow, black-haired thorax, contrasting strongly with the velvety black abdomen. Wings heavily browned, especially along veins. Legs black.

♀. *Head.* Frons proportions 12:12:108, index 9, constricted to eight units intermediately. Callus almost linear (Text-fig. 8). Tomentum of frons, subcallus, face, parafacials and buccae all golden yellow. Hairs of frons, face and parafacials sparse, dark brown. Beard yellow, but with some brown hairs on buccae. First two antennal segments dark reddish with black hairs, rest black. Palpi dark brown with black hairs.

Thorax. Mesonotum thickly covered with greenish yellow tomentum, pleura similar, browner ventrally. Hairs black, except propleural supra-alar, postalar, hypopleural tufts and hairs at sides of scutellum, which are golden yellow.

Abdomen. Velvety dark brown or black, with uniform, recumbent black hairs.

Legs. Entirely black or very dark red-brown, with entirely black hairs.

Wings. Heavily stained with dark brown, especially along veins, with some clearer areas in cells. Not noticeably paler at tip. Tegula with golden tuft.

Length. Body 20 mm.; wing 18 mm.

Type in the British Museum. There also are two female paratypes, Dutch New Guinea, Mimica R., Aug., 1910 (Wollaston); two females, Bivak-Elland (Lorentz Exped.); one female, "New Guinea", with no collector's name. One female in the British Museum from the Aru Islands, 1911 (Froggatt), has the third and later antennal segments bright orange, and has more yellow hairs on the pleura. This probably represents an island form.

Schuermans Stekhoven adds other records of the Lorentz Expedition, Etna Bay, Alkmaar, Kloofbivak, Regen Is.

TABANUS DOREICUS.

Tabanus doreicus Walker, 1861, *Proc. Linn. Soc. Lond.*, 5, p. 233; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 396; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 496.

Atylotus sonnerati Bigot, 1892, *Mem. Soc. zool. France*, 5, p. 672.

Ricardo remarks that all the known specimens of this species are faded and that in fresh specimens the tomentum of the thorax would probably be brighter and the contrast between it and the dark abdomen would be more pronounced. From *wollastoni* it is readily separated by the more orange antennae, the pale hairs of the mesonotum, and the unnarrowed first posterior cell.

♀. *Head.* Frons proportions 12:10:87, index 9, narrowest point seven units. Callus prominent, elongate, with spindle-shaped extension (Text-fig. 6). Tomentum of frons, subcallus, face and parafacials yellow. Dark hairs, brown hairs on buccae, face, parafacials and frons, though beard is mostly yellow. Palpi brown, with black hairs. Antennae (Text-fig. 6): first two segments orange with black hairs. The rest is missing in Walker's type; in Bigot's type third segment bright orange, others darker.

Thorax. Mesonotum and pleura thickly covered with greyish yellow tomentum. Mesonotum with short black hairs, freely mingled with pale yellow hairs, side margins with yellow tufts. Pleural hairs chiefly black, some yellow, on pteropleuron and in tufts around wing base.

Abdomen. Dorsally dark red-brown with black hairs, ventrally similar, but more dark brown.

Legs. Blackish brown, with black hairs.

Wings. In Bigot's type, uniformly brown. In Walker's type, darker along anterior veins and paler at tip. Ricardo mentions the variation in this respect.

Length. Walker's type: Body 17 mm., wing 16 mm.; Bigot's type: Body 14 mm., wing 13 mm.

I have seen three specimens of this species, all in the British Museum. Walker's type is from Doré (A. R. Wallace), and Bigot's type simply from "New Guinea". The third specimen is from Frühstorfer's collection and was recorded by Ricardo and Schuurmans Stekhoven as from "Keapaun", Dutch New Guinea. The MS label, however, is clearly either "Keipaur" or "Kapaur". I cannot find either of these in any gazetteer, but my lepidopterist colleagues in the British Museum, who have charge of much material collected by Frühstorfer, tell me that Kapoer or Kapaur is an earlier name for Fak-Fak in the Onin Peninsula (2° 55' S., 132° 17' E.).

Walker's and Frühstorfer's specimens are clearly similar. Bigot's is smaller and more uniformly brown in the wings. Ricardo also records one specimen in Kertesz's collections from Finsch Harbour at the other end of New Guinea.

TABANUS FLAVIPENNIS.

Tabanus flavipennis Ricardo, 1913, *Bijdr. Dierk.*, 19, p. 71; Schuurmans Stekhoven, 1924, *Treubia*, v, p. 299, and Boeroe-Publ., II, p. 1; 1926, *Treubia*, vi, suppl., p. 500.

A very distinct species, easily recognized by the dull black head, antennae, body and legs, and the rusty-yellow wings. Frons very narrow, index 9, narrowest point eight units, tapering very slightly toward antennae. Callus very long, almost linear (Text-fig. 29). Length of body 18 mm., of wings 18 mm.

This species has not yet been recorded from New Guinea, and seems to be confined to the island of Buru. There are three females, including the type, in the British Museum collection, and Stekhoven lists detailed localities within the island. He summarizes them thus: ". . . *Tabanus flavipennis* is a Tabanid belonging to the hill and mountainous region; it is found between 100 and 1,300 m. above sea-level, and prefers moist places."

TABANUS CINNAMONEUS.

Tabanus cinnamoneus Doleschall, 1858, *Natur. Tijds. Ned.-Ind.*, xvii, p. 84; Szitády, 1926, *Biol. Hung.*, 1, p. 13.

Tabanus ceramensis Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 377. *New Synonymy.*

A very distinctive species, in which the thorax is thickly yellow-tomented, abdomen dorsally bright orange with orange hairs, and ventrally shining black-brown with black hairs, legs black, wings dark brown. It was described from a unique male, and the females show some slight deviation.

♀. *Head.* Frons proportions 12:10:84, index $8\frac{1}{2}$, narrowest point nine units. Callus almost linear, shining reddish brown (Text-fig. 30). Tomentum of frons, subcallus, face, parafacials and buccae bright yellow; hairs black at vertex, otherwise bright yellow, including beard. Antennae: first two segments orange with black hairs, third segment bright orange with a strong tooth bearing a short tuft of black bristles, following segments black. Palpi lemon-yellow, but thickly covered with short black hairs.

Thorax. Mesonotum thickly covered with lemon-yellow tomentum and sparse erect black hairs intermingled with recumbent yellow ones. Pleura similar, more brown ventrally, hairs yellow.

Abdomen. Dorsally bright orange, extreme margins yellowish, orange hairs predominating, including lateral fringe, but black hairs visible beneath them. No pattern. Ventrally shining black-brown with black hairs, extreme margins reddish, with a short marginal fringe of orange hairs.

Legs. Front coxae yellow with yellow hairs basally, apically brown with black hairs. Other coxae brown with mostly black hairs. Legs black or very dark red-brown, with black hairs.

Wings. Very dark brown, paler at tip. First posterior cell slightly or strongly narrowed towards margin. Tegula with orange tuft.

Length. Body 19 mm.; wing 15 mm.

♂. See below.

The above description and the figure (Text-fig. 30) are taken from mainland specimens. The male from Hollandia is closely similar to these females, but Doleschall's and Stekhoven's types, both males, show some differences. They are smaller, have a more slender antenna, with a less pronounced tooth, and have the first posterior cell less strongly narrowed.

I am sure that *cinnamoneus* and *ceramensis* are the same species, but the mainland specimens may be a distinct species. I have not described them as new for the following reasons: the characters concerned are variable, and a male from Aru Is. is intermediate, having a more slender antenna, but a somewhat narrowed first posterior cell; the two male types are island specimens and would be expected to differ from the mainland form; I have no female to match with them.

Doleschall's type male, from Amboina, April, is labelled "1859". although the description was published in 1858. Perhaps this was an error for 1856. The type is in the Naturhistorisches Museum, Vienna, and was kindly lent to me by Dr. Max Beier. Stekhoven's type, a male also, is in the British Museum, and is from Ceram (Wallace). In the British Museum also are one female, Cyclops Mts., Sabron, 900 ft., v.1936 (Cheesman) and 1 female, Humboldt Bay Dt., Bewani Mts., ix.1937 (Stüber). In the Archbold Collection one female, Hollandia, vii.1938 (Toxopeus). In the School of Public Health and Tropical Medicine, Sydney, are one female, Mamberamo, Alb.-Bivak,

vii.1926 (v. Leeuwen), and the male from Aru Is., Elgner, 1911 (Froggatt), referred to above. In the Washington Collection are one male and two females from Hollandia, April, 1945 (Malkin).

TABANUS FURUNCULIGENUS.

Tabanus furunculigenus Doleschall, 1858, *Natur. Tijds. Ned.-Ind.*, xvii, p. 84; Szitády, 1926, *Biol. Hung.*, 1 (?), p. 13.

Tabanus obscuratus Walker, 1864, *Proc. Linn. Soc. Lond.*, viii, p. 232; Ricardo, 1912, *Bijdr. Dierk.*, 19, p. 71; 1913, *Nova Guinea*, ix, zool. 3, p. 389, *note*; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 468; 1932, *Arch. Naturg.*, 1 (1), p. 89.

A middle-sized (16 mm.) dark brown species, without any distinctive characters, separated from *pollinosus* Ric. mainly by its smaller size, and from *recusans* Walker by the absence of any bluish sheen at the base of the abdomen. The following description is taken from Walker's type specimen.

♀. *Head.* Frons proportions 12:10:83, index $8\frac{1}{2}$, narrowest point nine units. Callus almost linear (Text-fig. 7). Tomentum of frons, subcallus and face yellow-brown, hairs, including beard, dark brown. Antennae (Text-fig. 7) first two segments brown with black hairs, rest bright orange. Palpi brown with black hairs.

Thorax. Mesonotum brown, with brown, black and a few yellowish hairs (denuded in type). Pleura similar, entirely with black or dark brown hairs.

Abdomen. Dark brown with black hairs. No median triangles visible. Venter similar.

Legs. Dark brown with entirely black or dark brown hairs.

Wings. Brown colour distributed along veins. Tegula with black hairs.

Length. Body 16 mm.; wing 16 mm.

♂. Similar, wings more clearly pale at tips.

Stekhoven (1926) points out that the wings of the type are much lighter in colour than those of any other Ceram females, but that this may be due to fading of the type.

Doleschall's type, from Amboina, is in the Naturhistorisches Museum, Vienna, and was kindly lent to me for study by Dr. Max Beier.

In the British Museum are the holotype* of *obscuratus* female from Ceram (A. R. Wallace); four females from Ceram (various collectors) and one from Amboina 2-5.xi.1923 (C. J. Brooks); in addition there are four females from Ternate from Bigot's collection, where they stood as *furunculigenus* Dol.

In the School of Public Health and Tropical Medicine, Sydney, are four females, N. New Guinea, Pionierbivak, June-July, 1920 (v. Heurn); one male, N. New Guinea Exp., 1926, Motorbivak (v. Leeuwen); one female, Mamberamo, Albatros Bivak v, 1926 (v. Leeuwen). In the Archbold collection is one female from Araucaria Camp, 2,500 ft., 2.iv.1939 (Toxopeus).

Stekhoven records this species from Ceram and from the van Heurn collecting area at Pionierbivak and Prauwenbivak. He does not comment on the fact that the mainland New Guinea specimens have much more yellow hair on the mesonotum than the Ceram specimens. It is possible that two species are represented, but more likely that the two are merely geographical races.

TABANUS RECUSANS.

Tabanus recusans Walker, 1859, *Proc. Linn. Soc. Lond.*, 3, p. 83; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 397; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 507.

A medium-sized species, blackish, distinguished from *obscuratus* Walker by the plum-like bloom on the thorax and first two abdominal segments. A slight difference

* In a letter dated Nov., 1940, the late Mr. F. H. Taylor told me that he had located some of Francis Walker's types in the National Museum, Melbourne, among them being *T. obscuratus*, *T. exagens*, and *T. serus*. The specimens in the British Museum which I have quoted as types in this paper are part of the original material brought home by Wallace, and, since Walker did not commonly indicate holotypes, there seems to be no obvious way of deciding between the two sets of specimens. It would be better to regard them as co-types, unless any reason should arise for suspecting that they are not conspecific.

in venation can be seen in *recusans*; vein R_4 is flattened in its middle course, so that the tip of the first submarginal cell (cell R_{2+3}) is narrowest some distance from the end, instead of narrowing steadily towards the tip (Text-fig. 3). First posterior cell (cell R_5) not so much narrowed as in *obscuratus*.

♀. *Head*. Frons proportions 12:9:80, index 9. Callus as in Text-fig. 31. Frons with yellow tomentum and fine black hairs. Face with yellow-brown tomentum, hairs golden brown, beard darker brown. Antennae (Text-fig. 31): first two segments brownish orange with black hairs, third segment bright orange, following segments slightly darker. Palpi blackish brown with a purplish bloom and black hairs; stout at base, tapering to a long point.

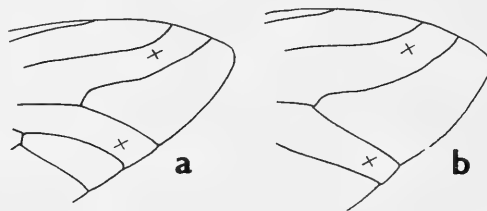
Thorax. Mesonotum grey-brown, with an overlying purple bloom; scutellum mahogany-red, humeri and notopleural calli orange. Upright fine black hairs and recumbent greenish yellow ones, lateral tufts largely pale. Pleura greyish with purplish bloom, hairs chiefly brown, but pale on propleuron.

Abdomen. Dorsum dark brown, first two segments with a purplish bloom; venter exactly similar. Hairs black, except centrally on first tergite, where they are pale.

Legs. Dark reddish, femora and tarsi darker than bases of tibiae, femora with some purplish bloom. Hairs dark brown or black.

Wings. Browned, paler at tip, with more or less distinct clouds on some of the cross-veins, especially on radial fork. Vein R_4 flattened (Text-fig. 3). Tegula with mixed pale and black hairs.

Length. Body 16 mm.; wing 14 mm.



Text-figure 3.

Tip of wing in: a, *Tabanus recusans* Wlk.; b, *T. obscuratus* Wlk., showing shape of cells R_{2+3} and R_5 .

In the British Museum are the holotype female from Aru Is. (A. R. Wallace) and one female from Waigeu, Camp Nok, 2,500 ft., iv.1938 (Cheesman).

In the School of Public Health and Tropical Medicine, Sydney, are four females from Angoram (S. H. Christian) and one female from Wewak (Curtis Deland).

Stekhoven records this species from Noordrivier (Lorentz), Salawatti Is., and Haroeka (? Haruku Is., Amboina group).

TABANUS VANLEEUWENI, n. sp.

A species differing from *obscuratus* and *recusans* in the browner coloration of abdomen and legs. The prothoracic hairs are white and the wings more strongly browned on the foreborder and at the base of the radial fork.

♀. *Head*. Frons proportions 11:9:67, index $7\frac{1}{2}$. Callus elongate (Text-fig. 37). A small bare spot near vertex. Tomentum of frons bronze-yellow, with black hairs. Subcallus tomented, pale brown, contrasting with face, parafacials and buccae, which are white. A few brown parafacial hairs anteriorly, rest of hairs snow-white. Antennae (Text-fig. 37): first two segments brown with black hairs, third segment bright orange, following segments black or blackish. Palpi white, with black hairs.

Thorax. Mesonotum blackish brown, with fine black hairs and sparse, pale yellow, scaly hairs. Humeri and notopleural calli orange. Pleura blackish, with white tomentum and mainly white hairs, a few black ones on mesopleuron.

Abdomen. Reddish brown, blackish towards tip. Hairs of dorsum black, those of venter whitish.

Legs. Reddish brown, femora and tarsi, especially those of forelegs, somewhat blackish. Hairs mainly black.

Wings. Somewhat browned all over, but more strongly so on foreborder, with a more or less distinct small cloud on base of R_1 . Vein R_1 slightly flattened, not so strongly as in *recusans*.

Length. Body 14 mm.; wing 12 mm.

In the School of Public Health and Tropical Medicine, Sydney, are two co-types, females from N. New Guinea, Mamberamo, Albatros Bivak, v and vii, 1926 (v. Leeuwen). In the Archbold collection one female paratype from Bernhard Camp, 150 ft., 19.ix.1938 (Olthof).

I have created these two co-types instead of one holotype because one specimen has lost the antennae and the other is greasy and discoloured, especially about the pleura.

TABANUS OPALESCENS.

Tabanus opalescens Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 513.

A distinctive species, almost uniformly blue-grey in colour, wings browned, frons strongly narrowed towards antennae (Text-fig. 34), thorax and abdomen rather elongate. It seems to belong near *obscuratus* Walk., but because the Japen specimen has very indistinct triangles of pale hairs on the abdomen I have included the species twice in the key.



Text-figure 3M.

Map showing distribution of *T. pollinosus* Ric. and *T. angusticallosus* Ric.

♀. *Head.* Frons proportions 13:7:73, index $10\frac{1}{2}$. Frons with slate-grey tomentum and black hairs, callus long and narrow, with a small lower expansion (Text-fig. 34). Subcallus with brown tomentum, contrasting with parafacials, face and buccae, which are grey with mainly black hairs; lower and inner part of beard white. Antennae (Text-fig. 34): first two segments brown, other black or blackish. Palpi blackish with black hairs.

Thorax. Mesonotum dark brown, but thickly overlaid with a blue-grey tomentum. Hairs fine black and recumbent yellowish, about equally mixed. Pleura similar in colour, hairs chiefly white, some dark hairs on mesopleuron.

Abdomen. Thickly covered with blue-grey tomentum. Hairs black on dorsum, white or whitish on sides, venter, and partly on dorsum of first segment. Near each side of this segment is a patch of thick black hairs which stands out among the white. The Japen specimen has very indistinct triangles of pale hairs on abdomen.

Legs. Coxae mainly with silvery hairs, fore coxae with a few black hairs apically. Femora black, with a bluish sheen like the thorax. Tibiae reddish brown basally, darker apically, tarsi also dark. Some white hairs ventrally on femora, other hairs black.

Wings. Almost uniformly browned, slightly darker anteriorly. Vein R_4 with moderately long appendix. Tegula with mainly pale tuft.

Length. Body 15 mm.; wing 12 mm.

Described from Heuvel Bivak (Lorentz), paratypes from Kloof Bivak, 31.10.1913 (Versteef). Type in Natura Artis Magistra, Amsterdam.

In the British Museum are three females, Humboldt Bay Dt., Bewani Mts., ix.1937 (W. Stüber); one female, "Hollandia", 140° E., 3° 10' S., 1,000–2,000 ft. (W. Stüber); one female, Japen Is., Mt. Eiori, 2,500 ft., x.1938 (Cheesman).

In the Archbold collection, one female, Hollandia, vii.1938.

TABANUS ILLUSTRIS.

Tabanus illustris Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 398; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 504.

A distinctive species with purplish black abdomen and contrasting bright red thorax. It can only be confused with the following species, *T. flammeus* S.S.

♀. *Head.* Frons proportions 15:13:85, index $6\frac{1}{2}$. Callus flask-shaped, median extension very long and rather thick (Text-fig. 16). Tomentum of frons silvery in certain lights. Tomentum of subcallus golden-brown; face, parafacials and buccae ashy, with brown hairs. Antennae (Text-fig. 16): black, first segment more greyish. Palpi blue-grey with black hairs, broad at base and tapering to a slender point (cf. *T. flammeus*).

Thorax. Mesonotum bright orange-red. Fine hairs black, a few short golden hairs, especially on the postalar calli and before the scutellum. Pelura red, thickly overlaid with a purplish tomentum; hairs mostly black, some pale on pronotum and on ptero- and metapleuron.

Abdomen. Dorsum and venter black, with a plum-like bloom. Hairs black, no pale median triangles.

Legs. Black, femora purplish, tibiae rather reddish. Hairs, including hairs of coxae, black.

Wings. Yellowish-tinted, rather darker on foreborder. R_4 with short appendix.

Length. Body 17 mm.; wing 15 mm.

In the British Museum is the holotype female from Iwaka R. (Wollaston). Stekhoven records one female from the Lorentz collection.

TABANUS FLAMMEUS.

Tabanus flammeus S.S., 1926, *Treubia*, vi, suppl., p. 505.

This species was created for four females from Heuvel Bivak (Lorentz), three of which were recorded by Ricardo as a form of her species *illustris*. I think Stekhoven is correct in regarding the differences as of specific value, and from the few specimens available it looks as if *flammeus* is the more widely distributed of the two. It differs from *illustris* in the shape of the callus and the darker tomentum of the frons; the shorter and stouter palpi; the white pubescence of beard and coxae; and the darker wings, with a longer appendix to R_4 .

♀. *Head.* Frons proportions 16:13:73, index $5\frac{1}{2}$. Callus flask-shaped, with stout median extension only half the length of the frons (Text-fig. 32). Tomentum of frons silvery-white beside lower callus, becoming blackish above, and purplish at vertex, upper part of frons with rather long black hairs. Hairs of face and parafacials dark brown, beard snow-white. Palpi shorter and plumper than in *illustris*.

Thorax. Mesonotum with yellowish hairs more abundant than in *illustris*, and pleura with predominantly white hairs.

Abdomen as in *illustris*.

Legs. As in *illustris*, but coxae and femora with long white hairs; femora with black hairs as well.

Wings. Markedly darkened in front, up to and including vein R_5 . Appendix of R_4 longer than in *illustris*.

Length. Body 14 mm.; wing 12 mm.

The holotype female from Heuvelbivak (Lorentz) is in *Natura Artis Magistra*, Amsterdam, and one paratype female from this locality is in the British Museum.

In the Harvard Museum, one female, Morobe district, Mt. Misim, 7,000 ft. (Stevens). In the Archbold collection is one female from Sigi Camp, 4,500 ft., 29.ii.1939 (Toxopeus). This is a subsidiary camp in the vicinity of Bernhard Camp (see Archbold *et al.*, 1939, p. 226).

TABANUS STÜBERI, n. sp.

A medium-sized, mainly black species, in which the mesonotum is grey and contrasts strongly with the black abdomen. It is less brown in appearance than *doreicus* Wlk., and has no appendix to R_4 .

♀. *Head.* Frons proportions 13:10:78, index 8. Callus as in Text-fig. 33. Tomentum of frons greyish brown, with black hairs, which are rather longer towards the vertex. Face, parafacials and buccae brown-and-grey tomented, hairs mostly brown, but beard white posteriorly. Antennae dull reddish on first two segments, rest black. Palpi blackish, with thin golden tomentum and black hairs.

Thorax. Mesonotum black-brown, with a grey tomentum which gives the whole an ashy appearance. Fine black hairs mingled with a yellowish-white pubescence, which is thicker on hind half. Notopleural tuft mainly black. Pleura more brownish than notum, with mainly brown hairs.

Abdomen. Dark black-brown, uniformly covered with black hairs, without pale median triangles.

Legs. Blackish brown, femora with a greenish sheen. Hairs black.

Wings. Browned, colour slightly stronger along veins, and paler in centre of cells, especially towards wing tip. Vein R_4 with short appendix.

Length. Body 15 mm.; wing 14 mm.

Holotype female, Humboldt Bay dist., Bewani Mts., ix.1937 (W. Stüber), in the British Museum.

Paratypes: In the Archbold collection two females, Bernhard Camp, 9.ix and 11.x.1938 (Olthof); in the U.S. National Museum, four females, five males, Hollandia, April, 1945 (Malkin).

All the specimens from Hollandia are immature, probably part of a newly emerged batch. For this reason I cannot say whether the male coloration differs from that of the female, but the two appear to be the same.

TABANUS SEMICIRCULARIS.

Tabanus semicircularis Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 392.

Tabanus semicirculus Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 335.

A middle-sized (15 mm.) species, brown and white, thorax with two narrow grey stripes, abdomen with white crescents at base of second segment, and four segment with a semicircular median white spot and white lateral margins.

♀. *Head.* Frons proportions 13:12:64, index $5\frac{1}{2}$, almost parallel-sided. Callus light brown, club-shaped, with linear extension extending almost half length of frons (Text-fig. 17). Tomentum of frons white, with some black and some silvery hairs. Subcallus and upper parafacials with golden tomentum, latter with some brown hairs; rest of face and buccae white, with silvery hairs. Antennae (Text-fig. 17) mainly black, somewhat reddish basally. Palpi shining white, with black hairs.

Thorax. Mesonotum red-brown with paler tomentum at sides and on two narrow longitudinal stripes. Hairs are chiefly black on darker areas and chiefly yellowish white on pale areas; notopleural tuft mainly blackish, supra-alar and postalar tufts and scutellar fringe yellowish-white. Pleura white with white hairs.

Abdomen. Dark brown with black hairs, more yellow on first segment. Extreme base of second segment has a pair of crescent-shaped transverse white bands, and the second to fifth segments inclusive have a roughly semicircular white median spot; lateral margins of first five segments white. Venter largely brownish, with brown hairs, but basally and laterally white with white hairs.

Legs. Coxae with silvery hairs. Femora brick-red, tips of tibiae and all tarsi blackish. Hairs of femora and undersides of tibiae largely white, the rest black.

Wings. Somewhat browned in front, with a brown spot at base of R_4 and at tip of discal cell. R_4 with moderately long appendix.

Length. Body 13 mm.; wing 12 mm.

In the British Museum are the female holotype and one female paratype, both from Madew, St. Joseph River, 2,000–3,000 ft. (Stalker). These were apparently the only specimens previously known. In addition there are now in the British Museum 21 females, Papua, Mafulu, 4,000 ft., xii.1933; one female, Papua, Mondo, 5,000 ft., ii.1934; one male, Cyclops Mts., Sabron, Camp 2, 2,000 ft., vii.1936 (all collected by Miss Cheesman); three males, two females, Humboldt Bay Dt., Bewani Mts., ix.1937; three males, "Hollandia", 140° E., 3° 10' S., Jan., 1937–8 (Stüber).

This seems to be a species of the mountains. The above records represent two "pockets", one in Papua and the other south of Hollandia. No doubt further collecting will unearth similar areas elsewhere.

TABANUS EXAGENS.

Tabanus exagens Walker, 1864, *Proc. Linn. Soc. Lond.*, vii, p. 205; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 390; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 337.

Distinguished from *semicircularis* Ric. by having the median abdominal spots triangular, with slightly concave sides, by the proportions of the antennal segments (Text-figs. 12, 17), and by the unclouded wings.

♀. *Head.* Frons proportions 13:10:70, index 7. Callus flask-shaped with a linear extension about half length of frons. Subcallus and most of facial area white (subcallus brown in some lights), with a transverse brown band running through bases of antennae. Hairs brown on this band, white elsewhere, including beard. Antennae (Text-fig. 12) black, bases of segments a little reddish. Palpi whitish, with black hairs.

Thorax. Brown, with cinereus tomentum. Grey stripes broad, leaving only a narrow band between them. Sparsely covered with fine, erect black hairs and recumbent whitish ones; a triangle of longer black hairs before scutellum, the whitish hairs otherwise longer posteriorly. Pleura with white tomentum and mainly white hairs.

Abdomen. Dark brown with black hairs, on which a pattern is formed of grey tomentum and whitish hairs. This pattern consists of a patch in middle of first segment, a large triangle on second, smaller ones on third and fourth, and a faint one on fifth. Segmentations and side margins are also narrowly white. Venter obscurely reddish and blackish, with black hairs and paler segmentations.

Legs. Blackish, a little brownish at the knees, femora with a bluish sheen. Coxae white-haired above, black-haired below, femora with some white hairs, otherwise legs mainly black-haired.

Wings. Clear, R_4 with short appendix.

Length. Body 14 mm.; wing 12 mm.

In the British Museum are the holotype female and one female paratype from Mysol (Wallace); three females from Lorentz's collection; one female, "New Guinea" (ex Bigot's colln.); two females, "Hollandia" (140° E., 3° 10' S.), 900–1,500 ft. (Stüber); two females, Humboldt Bay Dt., Bewani Mts., 1,200 ft., vii.1937 (Stüber).

In the Archbold collection are three females, Bernhard Camp (Olthof), one dated viii.1938, and the other 15.x.1938.

TABANUS ANGUSTILINEATUS, n. sp.

A species that, in general appearance, combines the characters of *semicircularis* Ric. and *exagens* Walk. It has an abdominal pattern like that of *exagens*, but the spotted wings of *semicircularis*. The shape of callus and antennae, however, show it to be a distinct species.

♀. *Head*. Frons proportions 10:10:63, index 6, parallel. Callus short, flask-shaped, with only a very short, fine linear extension (Text-fig. 44). Tomentum of frons, subcallus and entire facial area white, except that around bases of antennae there is a dark brown area extending to the eyes and fading out on to margin of face. This area has some brown hairs, otherwise facial hairs and beard white. Antennae (Text-fig. 44): black, basal segments rather reddish, segments 4-7 rather short. Palpi greyish or whitish, with mainly black hairs.

Thorax. Mesonotum and pleura reddish brown, patterned as in *exagens*.

Abdomen. Brown, somewhat reddish basally. Base of second segment and hind margins and side margins of other segments narrowly white; also white, white-haired triangles on second to fifth segments, one more than in *exagens*. Venter reddish with mostly white hairs.

Legs. Reddish brown, tarsi darker, femora with greenish grey dusting. Hairs of femora and tibiae largely white.

Wings. Faintly browned, with deeper colour near apex, and with small clouds on R_4 and at apex of discal cell.

Length. Body 14 mm.; wing 11 mm.

Holotype and six female paratypes from Angoram (Christian) are in the School of Public Health and Tropical Medicine, Sydney. One paratype female from Nazab, Markham R. valley, July, 1944 (Krombein) is in the U.S. National Museum.

TABANUS COHAERENS.

Tabanus cohaerens Walker, 1865, *Proc. Linn. Soc. Lond.*, viii, p. 177; Ricardo, 1912, *Bijd. Dierk.*, 19, p. 71; 1913; *Nova Guinea*, ix, zool. 3, p. 389; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 220.

Atylotus picticornis Bigot, 1892, *Mem. Soc. zool. France*, v, p. 671.

Atylotus alfourensis Bigot, 1892, *Mem. Soc. zool. France*, v, p. 672.

A rather small species (12 mm.), brown or dark brown, with the median spots of the abdomen more or less distinctly united into a parallel-sided stripe. This species seems to be widespread in New Guinea and rather variable. Two variants are here given specific rank: *divisus* Ric., separated by the absence of golden hairs on the mesonotum and a different antennal shape; and *approximatus*, n. sp., distinguished by its more tapering frons and darker colour.

♀. *Head*. Frons proportions 11:8:65, index 8. Callus club-shaped, elongate, brown, lighter at base. Tomentum of frons yellowish, more greyish towards vertex, with dark brown hairs. Subcallus and parafacials a golden brown, face and buccae white. Hairs similar in colour. Antennae orange with black hairs (Text-fig. 10). Palpi yellowish with black hairs.

Thorax. Mesonotum greyish brown with fine black hairs and recumbent yellowish hairs, the latter more numerous posteriorly and around scutellum. Pleura grey, hairs yellowish on upper sclerites, silvery on lower ones.

Abdomen. Yellow-brown with mainly black hairs. Hind margins and lateral margins with a few whitish hairs and each segment with an elongate median pale triangle; viewed from behind, these triangles unite into a narrow, parallel-sided median stripe.

Legs. Yellow-brown, femora slightly greyish; forelegs darker, with femora rather blackish and tarsi and tips of tibiae black. Middle and hind femora and inner faces of tibiae with yellowish hairs, otherwise hairs mostly black.

Wings. Pale yellowish, foreborder near apex is darker. Appendix very small or absent.

Length. Body 12 mm.; wing 11 mm.

In the British Museum are the holotype female, "New Guinea" (Wallace); one female from Lorentz's Rivierkamp; one female, Etna Bay (N.G. Exp., 1906); three females, Cyclops Mts., Sabron, 930 ft., iv.1936; one female, Lake Sentani, Ifar, viii.1936 (Cheesman). Also present are the types of Bigot's two species and four other females from his collection. Unfortunately, owing to Bigot's dislike of precise localities, his specimens are labelled simply "New Guinea".

In the School of Public Health and Tropical Medicine, Sydney, are two females, W. Papua, Kiwani Is. (Stewart); one female, Nth. N.G., Prauwenbivak, 1920 (v. Heurn); one female, Hollandia (coll. ?); one female, Angoram (Christian).

In the Archbold collection, five females, Hollandia, vii.1938 (Toxopeus).

Miss Ricardo records this species from Ceram (Mrs. L. F. de Beaufort).

TABANUS APPROXIMATUS, n. sp.

I erect this new species for a number of specimens from Angoram, which differ from *cohaerens* Wlk. in the more tapering frons, the more linear callus, the shape and colour of the antennae, and the slightly larger size and darker colour. That this is not merely a local form is indicated by the fact that a normal *cohaerens* was taken at Angoram by Mr. S. H. Christian (see above). It does not seem to be the same as the form of *cohaerens* from Mamberamo recorded by Shuurmans Stekhoven (1926, p. 222), although his Figure 92 shows both forms of callus. It differs from *brunneothorax* S.S. (Buru) in the shape of the frons and callus.

♀. *Head.* Frons proportions 10:6:70, index $11\frac{1}{2}$, tapering to little more than half as broad at antennae. Callus almost linear (Text-fig. 42), dark brown. Tomentum of frons grey or blackish, with mixed black and yellow hairs. Subcallus with brown tomentum, face, parafacials and buccae with white tomentum and white hairs. Antennae (Text-fig. 42): a deeper red than those of *cohaerens*, third segment rather broader, following segments together distinctly shorter.

Thorax. Mesonotum chocolate-brown, humeri and notopleural calli orange. Short black hairs, thickly mingled with greenish, recumbent hairs, which are thickest posteriorly. Pleura with grey tomentum and mainly white hairs, some yellowish near wing base, and a few black on mesopleuron.

Abdomen. Dorsum a darker mahogany-brown than *cohaerens*, with mainly black hairs; a few yellow hairs laterally and in inconspicuous median triangles which form only an indistinct stripe. Venter more yellow with mainly yellow hairs.

Legs. Reddish yellow, fore femora, tip of fore tibiae, and all tarsi darker, all femora with some greyish dusting. Femora with some rather long white hairs, tibiae with shorter hairs, partly yellow and partly black.

Wings. Membrane rather darker than in *cohaerens*, pale brown rather than pale yellow, a deeper brown anteriorly. No appendix in any of the specimens I have seen.

Length. Body 14 mm.; wing 12 mm.

In the School of Public Health and Tropical Medicine, Sydney, are the holotype female and four males, four female paratypes, all from Angoram (Christian).

TABANUS DIVISUS.

Tabanus divisus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 392; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 335.

Miss Ricardo says of *divisus* that it is distinguished from *cohaerens* Wlk. by being darker and by having the frons only half as broad at the antennae as it is at vertex. These differences also apply to my new species *approximatus*, and it may be that this is no more than a form of *divisus*. The two can, however, be separated,

because *divisus* is smaller; the pale hairs of the abdomen are white, not yellow; the median, white-haired triangles are continued into a stripe by a paler area of the ground-colour; the mesonotum has much less conspicuous recumbent golden hairs, and the first antennal segment is paler, relatively longer and narrower.

♀. *Head.* Frons proportions 10:7:62, index 9. Callus (Text-fig. 11) almost linear. Tomentum of frons pale yellowish, hairs black. Subcallus and adjoining parts of parafacials golden-brown, latter with a few black hairs. Rest of parafacials, buccae and face white, with white hairs. Antennae (Text-fig. 11): first segment pale yellow, relatively longer and narrower than in *cohaerens*; second and third segments bright orange, following segments slightly darker. Palpi tapering, white but on outer face with a blue-grey sheen and black hairs.

Thorax. Mesonotum grey-brown, humeri and notopleural calli orange. Clothed with fine, erect black hairs and a few recumbent golden yellow hairs are visible, but not nearly so conspicuous as in the two allied species. Pleura with the hairs mainly white, a few blackish on mesopleuron.

Abdomen. Ground colour dark brown, with base of second segment narrowly pale and a faint median pale stripe that can be seen under the microscope, but is not obvious to the naked eye. Hairs dark brown, except for whitish tufts laterally and a small triangle of whitish hairs in the middle of each segment. These triangles are easily seen, but not the pale stripe connecting them. Venter reddish basally, blackish apically, with hairs brown except on segmentations, where they are longer and whitish.

Legs. Reddish yellow, femora somewhat dusted. Fore femora, apical third of fore tibiae, and fore tarsi darker. Femora with some white hairs, otherwise hairs of legs mainly black.

Wings. Browned, faintly except along fore border and up to vein R_4 , where brown colour is darker.

Length. Body 12 mm.; wing 10 mm.

Apparently only the original type material of this species has yet been seen. It was "a long series of specimens" from various localities of the Lorentz Expedition, such as Lorentz R., Regen Is., Digul R., etc. Stekhoven says the type is in the British Museum, but one of the three specimens there is labelled "Paratype". There is nothing in Miss Ricardo's statement by which we could identify one particular specimen as the Holotype.

TABANUS LENTICULATUS, n. sp.

A middle-sized, blackish brown species, with a single row of fairly distinct median triangles, and dark wings. The third antennal segment is black, broad, with a prominent tooth, and the following segments relatively short.

♀. *Head.* Frons proportions 13:13:74, index $5\frac{1}{2}$, parallel. Callus broad, flask-shaped, with a stout linear extension (Text-fig. 35). Tomentum of frons white anteriorly, blackish posteriorly, with black hairs. Golden-brown tomentum about bases of antennae, otherwise tomentum of subcallus and facial area white or whitish. Parafacial hairs mainly black, hairs otherwise white. Antennae (Text-fig. 35): first segment very broad, with prominent dorsal angle; second segment small, with long dorsal lobe; third segment broad, with strong tooth, following segments compressed, totalling not more than half the length of the third segment. Palpi swollen basally, tapering rather quickly to a short point, white with black hairs.

Thorax. Mahogany-brown with dark grey tomentum, humeri and notopleural calli somewhat paler. Fine hairs black, mingled with recumbent yellowish hairs. Pleura grey, hairs mainly white, but some black on mesopleuron.

Abdomen. Dorsum mahogany-brown with blackish tomentum. Hairs black, except for a median triangle of pale hairs and pale lateral hairs on each of first five or six segments. Venter similar, with pale hairs on segmentations.

Legs. Reddish yellow, tarsi darker, femora with bluish grey dusting. Femora with long white hairs basally and posteriorly, shorter black hairs anteriorly and at tip. Tibiae with black hairs dorsally, some pale hairs ventrally.

Wings. Stained with brown, which is stronger along main veins, at tips of R_{2+3} and R_4 , at base of R_4 , and at apex of discal cell. No appendix. Tegular tuft mainly pale.

Length. Body 15 mm.; wing 13 mm.

Holotype female, Papua, Yule Is., iii.1934 (Cheesman), is in the British Museum. Paratypes from Port Moresby, one female, 30:iv:1947 (Sneddon), two females (Dr. Strong), all in the School of Public Health and Tropical Medicine, Sydney.

TABANUS PRODUCTUS, n. sp.

Closely allied to *patriarchus*, n. sp., and to *opalescens* S.S., but differing in the less tapering frons (Text-figs. 34, 38, 40) and in the shape of the antennal tooth.

♀ *Head.* Frons proportions 14:10:76, index $7\frac{1}{2}$, tapering. Callus rather broad, tapering above into stout linear extension (Text-fig. 38). Tomentum of frons yellowish anteriorly, blackish near vertex, with black hairs. Subcallus and upper parts of parafacials a golden brown, rest of facial area white. Hairs of parafacials black, other hairs white. Antennae (Text-fig. 38): black, third segment with a pronounced tooth, forwardly inclined. Palpi bluish grey with black hairs.

Thorax. Mesonotum grey-brown with reddish patches, humeri and notopleural calli reddish; seen from behind it has a bluish sheen. Erect, short black hairs, sparsely intermingled with recumbent yellow hairs. Pleura grey with faint bluish sheen. Hairs silvery white, except for a few black hairs on mesopleuron.

Abdomen. Dorsum black with a bluish sheen, noticeable on first two segments, but visible on all segments if they are seen from behind. Hairs black, yellow hairs only in very small and indistinct median triangles and on extreme side margins. Venter similar, but with yellow-haired segmentations.

Legs. Black, knees narrowly reddish, femora with a bluish sheen. Hairs mainly black, but white hairs posteriorly on femora.

Wings. Rather strongly browned, except for extreme tip, which is clear. R_4 with long and curved appendix.

Length. Body 13 mm.; wing 13 mm.

Holotype female, Bernhard Camp, 150 ft., 23.xii.1938; one female paratype, Araucaria Camp, 2,400 ft., 22.iii.1939 (both Toxopeus). Type in the Buitenzorg Museum, Java.

TABANUS TRUNCATUS, n. sp.

A small species (10 mm.) with grey-brown thorax and reddish brown abdomen, which bears a row of distinct median pale triangles; segmentations and side margins yellow-haired. Antennae black, third segment broad, following segments compressed together.

♀ *Head.* Frons proportions 10:10:55, parallel. Callus (Text-fig. 39) broadly flask-shaped, with a stout linear extension. Tomentum of frons whitish, more greyish towards vertex, with black hairs. Subcallus and facial area whitish, except for a golden brown area at the bases of the antennae. Parafacial hairs brown, others white. Antennae (Text-fig. 39): two basal segments dark red with black hairs, rest black; basal segments broad with prominent angle, third segment rather broad with blunt tooth, following segments shortened. Palpi rather bluntly pointed, white, with white hairs at base and black hairs over most of surface.

Thorax. Reddish, with dark brown and grey tomentum. Erect black hairs and recumbent silky yellow ones. Pleura greyish, with mainly pale hairs.

Abdomen. Dorsum reddish brown, with a black patch in middle of second segment. Hairs black; a row of large median triangles and narrow segmentations are yellow with yellow hairs. Venter reddish brown, mainly with black hairs, but with some yellow, especially on segmentation.

Legs. Reddish yellow, darker on tarsi, especially fore tarsi and tip of fore tibiae. Femora with some greyish dusting. Hairs mainly long and white on femora, shorter and yellow on tibiae, black on tarsi.

Wings. Only faintly yellowed, with more definite colour on all cross veins and on costa towards wing tip. R_4 without appendix.

Length. Body 12 mm.; wing 10 mm.

♂. Rather similar, but the terminal segments of the antennae are not so contrasting in colour with the rest, and the wing spots are not so distinct.

Holotype female, one male, one female paratypes from Angoram (Christian) are in the School of Public Health and Tropical Medicine, Sydney.

TABANUS PATRIARCHUS, n. sp.

A middle-sized (17 mm.) species, brown-black, with a distinct row of median white-haired abdominal triangles; antennae and femora black; vein R_4 with an appendix.

♀. *Head.* Frons proportions 15:10:78, index 8, strongly tapering. Callus with a small lower portion and a fine linear extension (Text-fig. 40). Tomentum greyish brown, hairs black. Subcallus and parafacials similar, face and buccae grey with white hairs. Antennae (Text-fig. 40): first two segments blackish above, reddish brown below and at base; third segment narrowly bright red at base, rest of antenna black. Palpi blue-black, hairs black.

Thorax. Mesonotum grey-brown with fine black hairs and numerous pale yellowish ones among them. Humeral tuft white, notopleural mainly black. Pleura grey, with mainly white hairs, some black on mesopleuron.

Abdomen. Dorsum dark brown with black hairs. Paler hairs at base of first segment, on side margins, and in shallow median triangles on other segments. To the naked eye these triangles are very prominent against the dark ground colour. Venter dark brown, but with more pale hairs, especially on segmentations.

Legs. Femora bluish black, middle and hind femora narrowly reddish at base and at tip. Rest of legs blackish, except for joints and basal third of fore tibiae. Hairs of femora mainly white, those of rest of legs mainly black.

Wings. Practically hyaline. R_4 with appendix of variable length.

Length. Body 16–17 mm.; wing 14 mm.

♂. Similar, except that antennae are slightly more slender.

Holotype female, four female and eight male paratypes from Araucaria Camp, 18–24.iii.1939 (Toxopeus) are in the Buitenzorg Museum, Java. In the British Museum are five males from 140° E., 3° 10' S., 900–1,800 ft., Jan., 1937–38, and three males from Humboldt Bay Dt., Bewani Mts., ix.1937 (Stüber); two females, Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938 (Cheesman).

This series is remarkable for the high proportion of males taken. The two Japen specimens, as usual, differ in small details.

TABANUS INFUSCATUS, n. sp.

Differs from *patriarchus*, n. sp., in the parallel-sided frons, the differently shaped callus (Text-figs. 40, 41), and the wings stained with dark brown, and usually without appendix.

♀. *Head.* Frons proportions 13:13:86, index 6½. Callus elongate, flask-shaped, narrowing into a long median extension (Text-fig. 41). Tomentum of frons yellow-brown, hairs black. Subcallus and parafacials yellow-brown with black hairs, face and buccae white with pale yellowish hairs. Antennae (Text-fig. 41): first two segments red-brown with black hairs, third and following segments missing in all female specimens available. Palpi bluish grey with black hairs.

Thorax. Mesonotum with tomentum and mixed black and pale yellow hairs. Pleura grey, with mainly white hairs, some black on mesopleuron.

Abdomen. Blacker than in *patriarchus*, with longer black hairs and only a few orange or yellow hairs in the median triangles and on lateral margins of segments. Venter similar, with orange-yellow hairs on segmentations.

Legs. Fore femora bluish black with mainly black hairs. Basal two-thirds of fore tibiae orange, rest of tibiae and whole of tarsi black, with mainly black hairs. Middle leg more reddish, base of femora and tarsi a little blackish, black hairs. Hind femora blackish, tibiae yellowish, tarsi slightly darker.

Wings. Basally and anteriorly heavily stained brown, colour spreading along veins to tip and forming a fairly distinct spot on base of R_4 . R_4 with an almost right-angled bend, but without appendix.

Length. Body 17 mm.; wing 15 mm.

Holotype female and one female paratype from Humboldt Bay Dt., Bewani Mts., 1,200 ft., vii.1937 (Stüber), and one male, Cyclops Mts., Sabron, 930 ft., iv.1936 (Cheesman) are in the British Museum. In the Archbold collection, one female, Bernhard Camp, 150 ft., viii.1938 (Olthof), seems to belong here, but has darker legs, brown pleural hairs, and an appendix to R_4 .

TABANUS SERUS.

Tabanus serus Walker, 1862, *Proc. Linn. Soc. Lond.*, vi, p. 20; Ricardo, 1912, *Bijd. Dierk.*, 19, p. 71; 1913, *Nova Guinea*, ix, zool. 3, p. 398; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 415.

Tabanus facilis Walker, 1864, *Proc. Linn. Soc. Lond.*, vii, p. 206.

Atyotus laglaisei Bigot, 1892, *Mém. Soc. zool. France*, v, p. 673.

A rather featureless, red-brown species, about 17 mm. long, the reddish abdomen with indistinct triangles of yellow hair, and the whole antennae orange. Within this definition there is considerable variation, and it is possible that a number of allied forms or species are involved. *T. rubriventris* Macq. has a broader frons and different callus (Text-fig. 13), and is darker brown in appearance. *T. daruensis*, n. sp., is perhaps only a form of *serus*, but is smaller and darker. The three type specimens of *serus*, *facilis* and *laglaisei* are all very faded, and the following description is mainly based on modern material.

♀. *Head.* Frons proportions 12:11:83, index $7\frac{1}{2}$, tapering towards antennae. Callus elongate, flask-shaped, diminishing smoothly into a long median extension (cf. *rubriventris*, Text-figs. 13, 15). Subcallus and parafacials golden-brown, latter with black hairs. Buccae and face white, with white hairs. Antennae (Text-fig. 15): bright orange, scarcely darkened at tip, first two segments with black hairs. Palpi whitish, with black hairs.

Thorax. Mesonotum grey-brown, with a fine brown line down the middle and with some yellow tomentum just before the scutellum. Fine, erect black hairs and recumbent yellow ones. Pleura grey with white hairs ventrally, more yellowish ones near wing base, some black hairs on mesopleura.

Abdomen. Dorsum red-brown, closely covered with short black hairs; yellowish hairs are present on segmentations, on side margins and in tiny median triangles. In rubbed specimens the abdomen looks brick-red, through the loss of the black clothing-hairs, and the median triangles may be lost. Venter similar, with longer yellow hairs on segmentations.

Legs. Some black hairs on coxae. Femora reddish, hind femora with a little blue-grey dusting. Hairs mixed, short black and longer yellowish. Tibiae and tarsi similar, with more numerous black hairs. Fore-legs with the tarsi and apical third of the tibiae darkened.

Wings. Stained yellow or pale yellow-brown, darkened at tips of veins and on fore margin, stigma clear yellow. No appendix, though R_4 has a right-angled bend.

Length. Body 16-17 mm.; wing 14 mm.

In the British Museum are the types of the three synonymic species, Walker's two types being from Mysol (Wallace) and Bigot's type from Waigeu. There are also one female, "New Guinea" (Wallace); two males from Papua, Kokoda, 1,200 ft.,

viii.1933; 13 females Waigeu, Camp Nok, 2,500 ft., iv.1938 (all Cheesman); one female, Bewani Mts., 1,200 ft., vii.1933 (Stüber). In the School of Public Health and Tropical Medicine, Sydney, are two females, Prauwenbivak, 1920 (v. Heurn); one female, Lae (Clinton); one female, Mamberamo, Albatros Bivak, v.1926 (v. Leeuwen).

The Archbold Expedition took a good series of this species at Bernhard Camp, Aug.-Nov., 1938 (Olthof) and April, 1938 (Toxopeus)—49 females in all; also one female, Araucaria Camp, 2,500 ft., 18.iii.1938 (Toxopeus).

TABANUS REBRIVENTRIS.

Tabanus rubriventris Macquart, 1838, *Mém. Soc. roy. Agric. Arts Lille*, 1838 (2), p. 135, and *Dipt. Exot.*, 1, p. 131; de Meijere, 1906, *Nova Guinea*, v, p. 74; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 417.

Tabanus novaeguineensis Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 399.

Very close to *serus*, but distinguished by having a broader, less tapering frons, the callus shorter and more square, reaching the eyes and not tapered smoothly into the linear extension, beard brown, fore femora blackish; third antennal segment more slender, tooth weaker (Text-fig. 13). Macquart in his original description says that the tarsi and tip of the tibiae of the hind legs are blackish, but an annotation by the late Major E. E. Austen queries whether this should not read: "anterieures" instead of "posterieures".

T. serus Wlk. may be no more than a form of *rubriventris*, but the differences are clear-cut. There is, for example, no difficulty in picking out the single Waigeu specimen of *rubriventris* from the series of *T. serus* from the same locality.

Macquart's type of *rubriventris* was from Papua, Offak. No locality is given by de Meijere for his material. Ricardo's type of *novaeguineensis* was from Lorentz R., Bivak Is. In the British Museum are two female paratypes of *Novaeguineensis* from Bivak Is., and one female from Waigeu, Camp Nok, 2,500 ft. (Cheesman).

TABANUS INDISTINCTUS.

Tabanus indistinctus Bigot, 1892, *Mém. Soc. zool. France*, v, p. 639, Ricardo, 1911, *Nova Guinea*, ix, zool. 3, p. 394; Schuurmans Stekhoven, 1926, *Treubia* vi, suppl., p. 382.

Represented by a single female specimen, which must have been quite immature when caught, and which is now shrivelled. The colour of the hair is fairly well defined, but the coloration of the sclerites and the wings has probably never been properly developed. It is therefore useless to describe the colours of tomentum or sclerites.

♀. *Head.* Frons proportions 12:9:69, index $7\frac{1}{2}$, tapering. Callus (Text-fig. 14) pale yellow. Hairs of frons, parafacials and beard dark brown, face with some long brown hairs scattered over it. Antennae (Text-fig. 14): with black hairs, apparently first two segments are brown, third somewhat orange basally, darkened apically, terminal segments darkened. Palpi with black hairs.

Thorax. Mesonotum with longish black hairs, perhaps some silky yellow ones intermingled; postalar calli with some whitish hairs. Pleura with mainly brown or brownish hairs, white tuft on metapleuron.

Abdomen. Dorsum with black hairs, whitish hairs only in small median and lateral triangles, and sparsely along hind margins of segments. Venter with black hairs and thick marginal fringes of whitish hairs.

Legs. With entirely black hairs.

Wings. Appear entirely clear, though it may be that the colour has not developed. Veins pale yellow. R_4 with short appendix.

Length. Body 14 mm.; wing 12 mm.

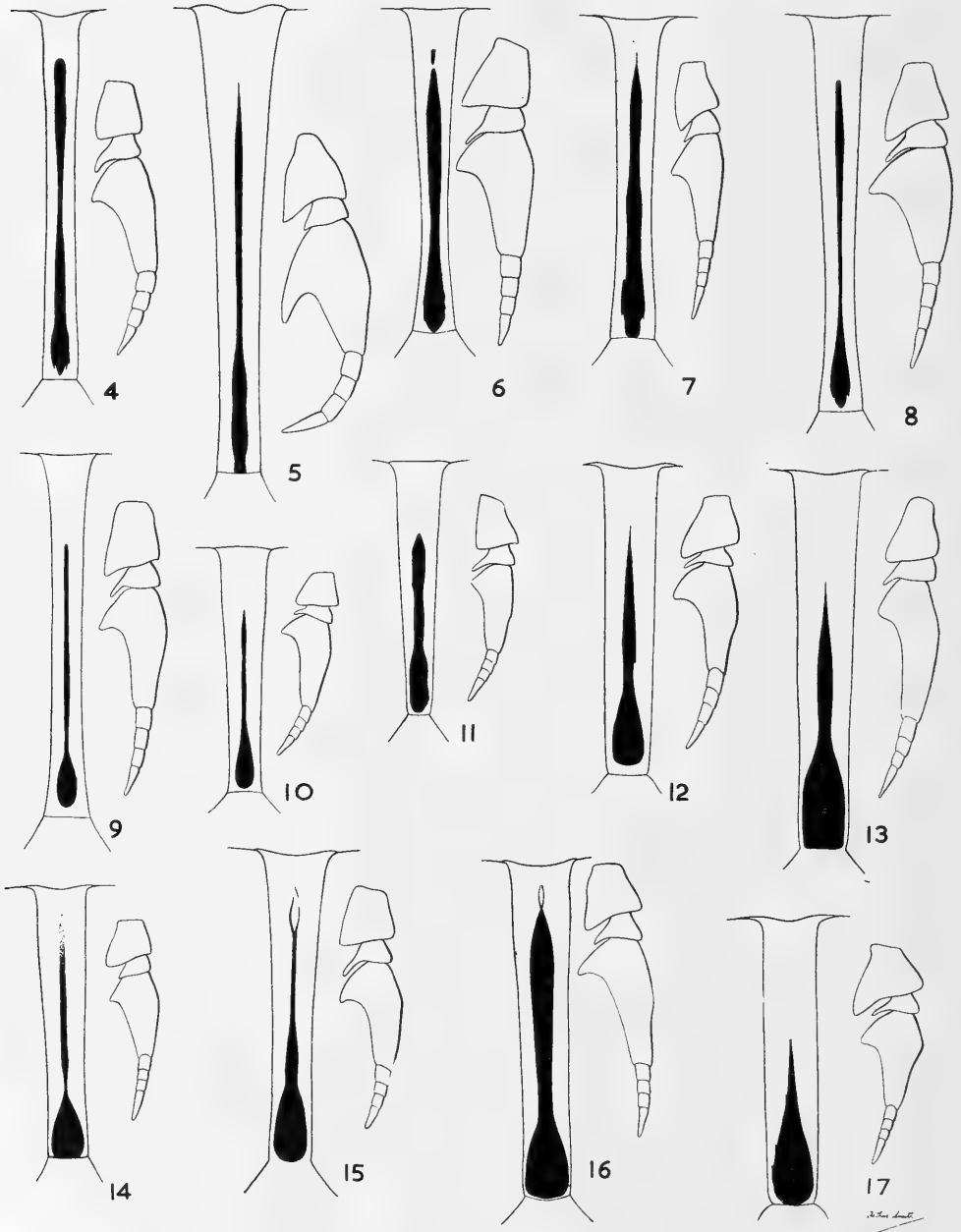
Holotype ♀ from Doré (Laglaise) is in the British Museum.

I am not able to throw much light on the identity of this species. Stekhoven compares it with *divisus* Ric., but I am more inclined to place it near to, if not as a form of, *serus* Walk. The short, dark beard is a difference. In this respect it agrees with *rubriventris* Macq., but has not the elongate third antennal segment, nor the yellow abdominal triangles of that species.

TABANUS DARUENSIS, n. sp.

Smaller than *serus* or *rubriventris*, with a different structure of antennae and palpi.

♀. Head. Frons proportions 13:11:72, index $6\frac{1}{2}$. Callus as in Text-fig. 43. Tomentum of frons yellowish anteriorly, black at vertex, with black hairs. Subcallus with pale golden tomentum, parafacials, face and buccae white, with white hairs and beard.



Text-figures 4-17.

Figs. 4-17. Frons and antenna of female: 4, *T. angusticallosus* S.S.; 5, *T. aurivittatus* Ric.; 6, *T. doreicus* Wlk.; 7, *T. furunculigenus* Dol.; 8, *T. wollastoni* Ric.; 9, *T. pollinosus* Ric.; 10, *T. cohaerens* Wlk.; 11, *T. divisus* Ric.; 12, *T. exagens* Wlk.; 13, *T. rubriventris* Macq.; 14, *T. indistinctus* Big.; 15, *T. serus* Wlk.; 16, *T. illustris* Wlk.; 17, *T. semicircularis* Ric.

Antennae (Text-fig. 43): terminal segments unusually long; first segment brown, with black hairs, and a little tuft of light orange hairs dorsally at tip; second segment orange with black hairs; third and succeeding segments orange.

Thorax. Grey-brown. Humeri and notopleural lobes orange, and an orange spot on each side of the scutum, on the transverse suture; margin of scutellum obscurely reddish. Fine black hairs rather dense, recumbent pale hairs rather longer than usual, but not very conspicuous, except posteriorly. Pleura grey, with mainly grey hairs, except for a few black ones on mesopleuron.

Abdomen. Dorsum orange or reddish, with pale segmentations and pale median triangles. Hairs pale yellowish on pale areas, black elsewhere. Venter basally yellow, apically blackish with black hairs and with white hairs rather abundantly on the hind margins of the segments.

Legs. Fore femora blue-greyish, other femora with a little blue-grey dusting. Legs otherwise yellow, with tarsi slightly darker.

Wings. Only very slightly browned along some of the anterior veins. No appendix to R_1 .

Length. Body 14 mm.; wing 12 mm.

Holotype one female, three female paratypes, Daru, Jan., 1927 (Nicholson). Other paratypes: two females Yule Is., Jan., 1927 (Nicholson); one female Wewak (Deland).

TABANUS RUFINOTATUS.

Atylotus rufinotatus Bigot, 1892, *Mém. Soc. zool. France*, v. p. 673; Ricardo, 1914, *Ann. Mag. n. Hist.*, (8) 14, p. 392; 1917, *Ann. Mag. n. Hist.*, (8) 19, p. 219; Hill, 1921, *Bull. ent. Res.* 12, p. 41; Schuurmans Stekhoven, 1926, *Treubia* vi, suppl., p. 148.

Tabanus designatus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 390; *1912, *Tijdsch. Ent.*, 54, p. 349.

This species is clearly distinguished from any other in New Guinea by its grey colour and the three rows of very conspicuous triangles on the abdomen. It is an offshoot of the Australian fauna, and is common and widely distributed in northern and eastern Australia. For these reasons I have not redescribed it, nor given a detailed synonymy. I understand that Mr. G. H. Hardy intends to do this in his forthcoming paper.

The known New Guinea distribution is Etna Bay and Merauke (Koch: type material of *designatus*. Two paratypes are in the British Museum). In the material from the School of Tropical Medicine, Sydney, is one male from Papua, Port Moresby, 2.i.1918 (no collector's name). These three are isolated coastal localities, but on the mainland this is not exclusively a coastal species. An account of its biology has been given by Hill (1921, *Bull. ent. Res.*, 12, 41-62).

TABANUS CEYLONICUS.

Tabanus ceylonicus Schiner, 1868, *Novara Reise*, Dipt. 93, p. 33; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 431; Nieschultz, 1931, *Zbl. Bakt.*, (2) 83, pp. 120-125.

Tabanus kershawi Ricardo, 1917, *Ann. Mag. nat. Hist.*, (8) 19, p. 221.

♀. **Head.** Frons proportions 11:8:63, index 8, tapering towards antennae. Callus rectangular, with incised upper border and moderately long median extension (Text-fig. 36). Subcallus slightly swollen, bare, and shining mahogany-brown. Face with light brown tomentum and black hairs. Parafacials dark brown with black hairs, beard black. Palpi dark brown with black hairs.

Thorax. Mesonotum dark brown with black hairs, humeri and parts of postalar calli yellowish. Pleura chocolate-brown, with dark brown hairs.

Abdomen. Dorsally and ventrally dark brown with black hairs, no pattern.

Legs. Femora, tip of fore tibiae and whole of fore tarsi dark brown. Rest of legs white, tips of segments being somewhat reddish yellow. Hairs on darker areas black, those on paler areas white.

* This note, synonymizing *designatus* with *rufinotatus*, was published before the description of *designatus* had appeared on print. *T. elesteem* Summers and *T. lineatus* Taylor are also synonyms, but full references to them are omitted because they concern only the Australian fauna.

Wings. Moderately stained yellowish brown, a heavier patch about middle of R_{2+3} . Costal cell clear yellow.

Length. Body 11 mm.; wing 10 mm.

This species stands apart from all the other Tabanidae occurring in New Guinea. By its striking appearance it would seem isolated enough to justify erecting a separate genus, but its characters are almost entirely chromatic rather than structural. Its range extends from Ceylon through the East Indies to the Solomon Islands and N. Queensland, so that it represents an intrusive element in the New Guinea fauna. Its true systematic position should be determined in relation to Oriental species. For the purposes of this paper it is better to leave it as an isolated member of the genus *Tabanus*.

The variety *nitidulus* Big. has a brown abdomen and yellow hair on the mesonotum. Nieschultz (1931) has described and figured the larva and pupa of this species.

The New Guinea specimens I have seen have the following localities: In the British Museum, one male (var. *nitidulus*), Merauke; 18 females Admiralty Islands (Taylor); six females, Cyclops Mts., Mt. Sabron, 900 ft., v.1936 (Cheesman); one female, Lake Sentani, Iffar, viii.1936 (Cheesman). In the School of Public Health and Tropical Medicine, Sydney, are 23 females, Manus Is., Admiralty Islands (Deland); three females, Kavieng, New Ireland (Taylor); one female Sauri, Wewak (Taylor); one female Idenburg R., Ter Poorter (1911); one female Boeroe, Denig, viii.1913. In the Archbold Collection 13 females, Bernhard Camp, 150 ft., ix.1938 (Olthof). In U.S. Nat. Museum Collection, one female, Cyclops Mts., 1,000 ft., April, 1945 (Jean Laffoon). In the S. Australian Museum two females, Torricelli Mts., 200-1,000 ft., Jan., 1939 (Cheesman); two females, Krisan, Vanimo, April, 1939 (Cheesman).

The New Guinea localities quoted by Stekhoven are the Lorentz area, Etna Bay, Prauwen Bivak, Merauke, Hollandia and the Idenburg River.

GENUS NEOBOLBODIMYIA.

Neobolbodimyia Ricardo, 1912, *Nova Guinea*, ix, zool. 3, p. 402; Schuurmans Stekhoven, 1926. *Treubia* vi, suppl., p. 135. Genotype: *N. nigra* Ricardo by original designation.

This is an isolated and little-known genus, founded for one specimen from the Lorentz collection, and distinguished by having not only a bulbous subcallus, upon which the antennae stand, but a greatly swollen first antennal segment as well. These swellings of the frons and its appendages occur sporadically in otherwise dissimilar species, and it is difficult to know when they really indicate relationship. In this instance the body-shape and heavily patterned wings, combined with the head characters, justify the genus, but, in spite of its name, it is not closely allied to *Bolbodimyia* from S. America.

N. veitchi Bezzi, from Fiji, was described in this genus because it has swollen first antennal segments, but it differs in many other ways, as Bezzi points out. I do not think it belongs in *Neobolbodimyia*. Similar considerations apply to *N. laticornis* S.S. and *N. argentata* Szilady, both from Celebes, neither of which is known to me.

NEOBOLBODIMYIA NIGRA.

Neobolbodimyia nigra Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 403; Surcouf, 1921, *Genera Insectorum*, 175, Tabanidae, p. 94.

This species is hitherto known from the unique female type, which has been independently described by Ricardo (1913), Surcouf (1921) and Stekhoven (1926). The type locality is "Bivak Island", which I assume to be one of the camp sites of the Lorentz Expedition, somewhere in the general area of Regen Island and the Lorentz R. (05°S, 139°E). Surcouf misquotes this as: "Île Bivals (Archipel de la Nouvelle Guinée)" at the beginning of his account, and at the end adds: "Type: un exemplaire femelle de la Nouvelle-Calédonie". I am not clear whether the latter is a mistake, or whether "Type" refers to an additional specimen seen by him.

The two specimens before me are males, so I am able to give a description of this sex. I have not seen the female, but from descriptions the male differs in having lateral thoracic patches of yellow hair, and in its general mahogany colour instead of black.

♂. *Head.* Eyes contiguous, clearly divided into a lighter brown upper area of large facets and a darker brown lower area of small facets. Dried specimens show no trace of the eyebands. Face reddish brown with white tomentum, slightly bulbous, with median groove. Parafacials black with white tomentum and dark brown hairs. Occiput similar, with yellow hairs. Antennae standing on a very prominent bulbous callosity, which is shining mahogany-brown, with brownish tomentum beneath. First antennal segment bulbous, one and a half times as long as its greatest width, shining mahogany-brown with black hairs; second and third segments about half as thick, *Tabanus*-like in shape, pale yellow, with black hairs. Palpi short, first segment blackish, second segment swollen, pointed at tip, orange with black hairs. Proboscis short, labella broad, reddish.

Thorax. Shining mahogany-brown, faintly dusted on dorsum and more thickly on pleura. Hairs long, silky and dark brown, except for a tuft of shorter, thicker, yellow hairs on each notopleural lobe.

Abdomen. Shining mahogany-brown with black hairs, tufted on side margins.

Legs. Reddish, with black hairs, femora and coxae darker. Hind tibiae and tarsi with a posterodorsal fringe of short red hairs.

Wings. As in female, dark brown, with an apical clear area covering a little of first submarginal cell and tips of second submarginal, first, second and third posterior cells. Clear spots at base of basal cell, and in centre of fifth posterior cell, and a clear streak crossing basal cells at beginning of discal cell.

Length. Body 13 mm.; wing 12 mm.

The female holotype is in *Natura Artis Magistra*, Amsterdam. In the British Museum are two males from 140°E, 3°10'S, 900–1,800 ft. (Stüber).

Genus PARACANTHOCERA.

Paracanthocera Enderlein, 1923, *Deutsch. ent. Zeitschr.* 1923, p. 545; *Mitt. zool. Mus. Berlin*, 11 (2), p. 332; Ferguson, 1926, *Bull. ent. Res.*, 16 (4), p. 301. Genotype: *Acanthocera australis* Ric., by original designation.

This genus, as understood by Enderlein, rests upon a misapprehension. The third antennal segments of Ricardo's type and paratype were missing when the species was described, and her reasons for placing the species in the genus *Acanthocera* were that: "Owing to the strong general resemblance, especially in the markings of the wings . . . (it) . . . no doubt belongs to this genus." A specimen in the British Museum from Kuranda, N. Queensland (Dodd), agrees with Ricardo's type, but has antennae quite unlike those of *Acanthocera*, and without any tooth-like projection. This removes the species from Enderlein's tribe Acanthocerini into his Diachlorini.

Ferguson (1926) says: "*Paracanthocera* . . . will probably prove valid, but it is doubtful if the actual species is known to Enderlein." This is a fair statement of the position: the genus should be retained, but needs to be redefined, from the type species.

In Enderlein's tribe Diachlorini this species runs to *Lissimas* End., but differs from the description of that genus in the shape of the palpi and in the type of wing pattern. The distinguishing characters of *Paracanthocera* are: the long first antennal segment, 3.3 times as long as its greatest width, almost parallel; frons index 4. No ocelli or ocellar tubercule. Callus pear-shaped and distinctly swollen in profile. Subcallus not swollen, rather bare. Face swollen, bare, shining. Proboscis short. Palpi same length as proboscis, much swollen basally. Wings mainly brown, with clear spots.

The type of *Chrysops parallelus* Walk. is in very bad condition. It has no head, the right wing is lost, and the left wing very badly torn. It seems clearly very close to *P. australis*, but the following difference can be seen: clear spot at base of basal cell smaller, that at extreme base of cell R₁ does not extend beyond beginning of R₂₊₃, and is even then not completely clear; brown colour fills basal third of cell R₄, and generally seems to extend nearer to the wing border. Admittedly I risk falling into the same error as Miss Ricardo when I assume the generic position of this headless and broken specimen, but the probability of being correct seems a little stronger.

P. australis Ric. occurs in N. Queensland, and *P. parallelus* Wlk. was described from Batjan Is., in the Malay Archipelago. I have not seen the genus among New Guinea material.

Genus CHALYBOSOMA, gen. nov.

Genotype: *Tabanus metallicus* Ricardo, by present designation.

Eyes bare. Frons almost parallel-sided, very slightly widened towards antennae, index about 4. Callus elongate, club-shaped (Text-figs. 18, 57, 58). Vertex thickly tomented, no ocelli nor ocellar callus. Subcallus moderately swollen, bare, and shining brown. Face bare, and shining in middle, and in a spot near each tentorial pit. Antenna *Tabanus*-like, but first segment rather elongate, slightly longer than broad in side view, third segment slightly elongate, but with distinct tooth (Text-figs. 18, 57, 58). Palpi elongate, tubular. Proboscis little longer than palpi, labella occupying half total length of proboscis. Thorax and abdomen more or less extensively metallic green or blue, with some non-metallic pale areas. Legs mainly dark, tarsi with sharply contrasting white basal area, not appreciably flattened. Wing mainly hyaline, anal cell distinctly closed and stalked. Subepaulet bare.

I erect this genus for a group of metallic green or blue species. Metallic coloration is not peculiar to these species of the Tabanidae, and, indeed, occurs sporadically in other predominantly non-metallic families, such as the Asilidae and Syrphidae, but in conjunction with the structural details given above it, serves to separate off three New Guinea species from the rest. I am not prepared to say that *T. cyaneus* Wied., from Queensland, should be referred to *Chalybosoma*; it is larger and more robust in build, and the first antennal segment is stouter.

KEY TO THE SPECIES OF CHALYBOSOMA.

1. Mesonotum extensively dull yellow at sides, and before scutellum, rest of mesonotum and scutellum metallic. Vein R_4 with very short appendix *malkini*, n. sp.
Mesonotum entirely metallic, except for humeri and notopleural lobes, no extensive yellow areas to be seen from above. Abdomen entirely metallic or with a pale transverse band basally. Vein R_4 without appendix 2
2. Abdomen entirely metallic, or with only a faint trace of pale, non-metallic colouring at base of second segment. Antennae uniformly orange, including terminal segments. Palpi black-brown or black-haired *metallicum* Ric.
Abdomen with a distinct, pale, non-metallic transverse band at base of second segment. Antennae more brownish, terminal segments distinctly darker. Palpi white-haired *luciliaeformis* S.S.

CHALYBOSOMA METALLICUM.

Tabanus metallicus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 393; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 503.

♀. *Head*. Frons proportions 12:13:48, index 4. Callus dark brown with thick linear extension (Text-fig. 18). Vertex with a thinning of the tomentum, but without ocelli or ocellar callus. Subcallus bare and shining, paler brown, only tomented along eye-margins. Central area of face, and a small spot adjoining tentorial pit on each side, is bare, shining pale brown. Rest of frons and face with yellowish white tomentum and pale yellow hairs. Antennae (Text-fig. 18): First two segments pale brown with black hairs above, yellow ones below; third segment bright orange with fine white hairs, remaining segments only slightly darker. Palpi brown with brown or black hairs. Proboscis little longer than palpi, labella being about half total length.

Thorax. Humeri orange with yellow hairs; notopleural lobes pale yellow with conspicuous yellow hairs and a small tuft of black hairs just before wing-base; postalar callosities dull reddish with black hairs. Pleura less completely metallic, with a number of pale areas. Hairs black in a stripe from notopleuron down over mesopleuron and sternopleuron, elsewhere yellow or whitish. Stekhoven refers to: "A black-haired patch . . . just underneath the wings", which he contrasts with the yellow hairs in that position in *luciliaeformis*. This must presumably refer to the black hairs on the mesopleuron (i.e., strictly before the wing), but these are also black in the specimens I identify as being *luciliaeformis*.

Abdomen. Metallic blue-green, with black hairs. Slightly reddish on anterior margin of first and second segments, and more extensively so ventrally.

Legs. Dark brown or black, with black hairs. Tibiae basally white with white hairs. White area of tibiae is one-half on foreleg, two-thirds on middle, and one-quarter on hind leg.

Wings. Clear, except for stigma and for brown colour filling the whole of the costal and first basal cells, most of second basal, and a little of anal.

Length. Body 9 mm.; wing 9 mm.

In the British Museum, one holotype female, Iwaka R. (Wollaston).

CHALYBOSOMA LUCILIAEFORMIS.

Chalybosoma luciliaeformis Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 504.

Differs from *metallicum* Ric. in the characters given in the key. I have already mentioned that Stekhoven says there is a white-haired tuft "just underneath the wings", but in my specimens the pleural hairs are like those of *metallicum*.

This species was founded for two paratypes of *metallicum* Ric., which are in Natura Artis Magistra in Amsterdam, and which I have not seen. The type-locality is Alkmaar. In the Archbold collection are two females, one male from Araucaria Camp, 2,400 ft., 15-22.iii.1939 (Toxopeus). The male is very like the female, but the eyes have a dense, silvery pubescence.

CHALYBOSOMA MALKINI, n. sp.

Has a transverse pale band on the second abdominal segment, and is very similar to *luciliaeformis* in nearly every detail, except the two mentioned in the key. At first I was inclined to regard these specimens as immature examples of *luciliaeformis*, in which the metallic colour of the thorax was not fully developed, but this would not explain the presence of an appendix to R₄. The colour differences are quite constant in specimens from very different localities. Moreover, the male of *luciliaeformis* and the male of *malkini* are both from the same locality, same date, both immature, yet they show quite clearly the differences cited. The eyes have silvery hairs.

Holotype female, one female paratype Hollandia, April, 1945 (Malkin), are in the U.S. Nat. Museum. In the Archbold Collection one male from Araucaria Camp, 7,500 ft., 18.iii.1939 (Toxopeus). In British Museum, one female paratype, Papua, Kokoda, 1,200 ft., vi.1933 (Cheesman).

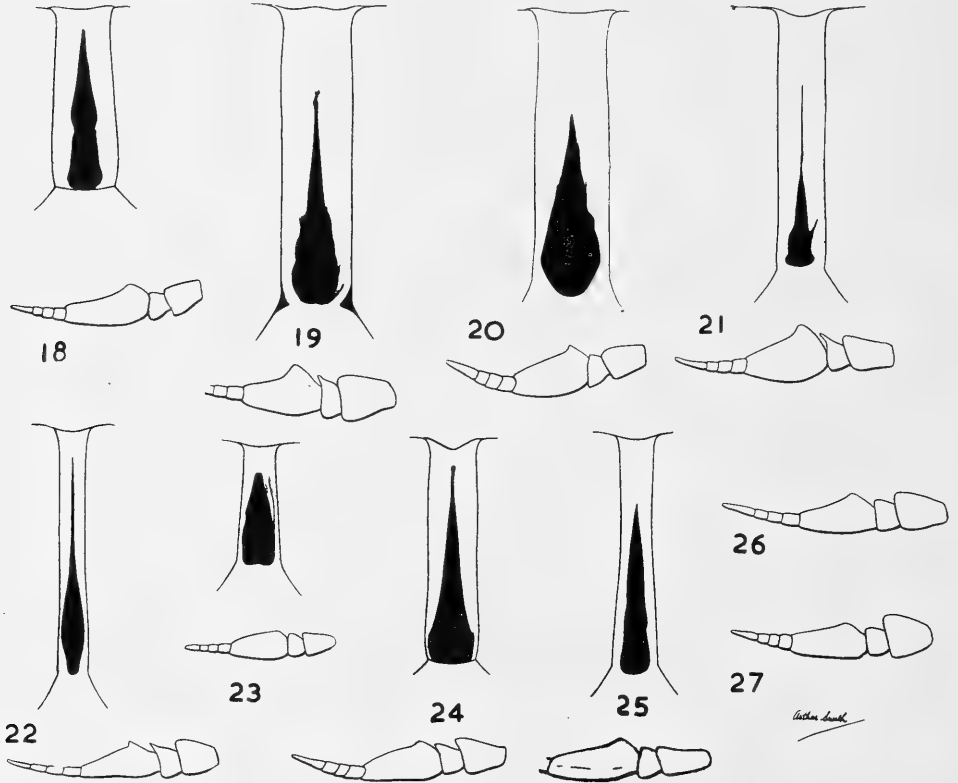
Genera CHASMIA and CHASMIELLA.

Chasmiella } Enderlein, 1922, *Mitt. zool. Mus. Berlin*, 10 (2), p. 344; 1925, *Mitt. zool. Musm.*
Chasmia } *Berlin*, 11 (2), p. 331.

KEY TO SPECIES.

1. First antennal segment twice as long as thick, cylindrical. Third antennal segment nearly parallel-sided, tooth insignificant. (One species: dark brown, notopleural lobes white, abdomen with white transverse band overlapping first and second segments, and a narrower band at hind margin of second segment.) CHIASMA End. (*basifasciatus* de Meij. = *bicincta* End.)
- First antennal segment not twice as long as thick, subtriangular, as in *Tabanus*. Third antennal segment with more or less distinct tooth CHASMIELLA End. 2
2. Mesonotum without conspicuous stripes, though the median third may be darker than the sides. Scutellum not strongly contrasting with mesonotum 3
- Mesonotum with three conspicuous black stripes on a yellow ground. Scutellum black, contrasting strongly with mesonotum 9
3. Pleura unicolorous, yellow or grey 4
- Pleura not unicolorous, but with a vertical brown stripe passing down mesopleuron, just in front of wing base 7
4. Pleura grey. Radial fork rectangular, with a suggestion of appendix *papouinus* Wlk. Pleura yellow. Radial fork shallow, no appendix 5
5. Almost the whole frons bare and shining, only a small area of tomentum near the median ocellus *ochrothorax* S.S. Shining callus not taking up whole of frons 6
6. Palpi (♀) yellow, with yellow hairs. Stigma clear yellow-brown *subhastata*, n. sp. Palpi (♀) blackish, with black hairs. Stigma dark brown *parva*, n. sp.

7. Face bare and shining *fulgidus* Ric.
 Face tomented, not shining 8
8. Smaller (7 mm.), dark brown species. Abdomen shining dark brown, first segment with pale hind margin and with white hairs centrally *raffrayi* Bigot
 Larger (9 mm.), pale species. First to third abdominal segments yellow both dorsally and ventrally *breviusculus* Wlk.
9. Mesopleura partly brown, with black hairs posteriorly. Fore femora blackish, contrasting with yellow coxae *fasciata*, n. sp.
 Mesopleuron entirely yellow, with yellow hairs. Fore femora mainly yellow, like coxae, but darkened at tip *parvicallosa*, n. sp.



Text-figures 18-27.

Figs. 18-27. Frons and antenna of female: 18, *Chalybosoma metallica* Ric. (subcallus not shown); 19, *Cyd. lorentzi* Ric.; 20, *Cyd. albithorax* Ric.; 21, *Cyd. sol.* S.S.; 22, *Cyd. solomonensis* Ric.; 23, *Chasmiella fulgidus* Ric.; 24, *Cyd. laetus* de Meij.; 25, *Ch. raffrayi* Big. (type). Antenna of male: 26, *Ch. papouinus* Wlk.; 27, *Ch. insurgens* Wlk.

CHASMIA BASIFASCIATA.

Tabanus basifasciatus de Meijere, 1915, *Tijdschr. v. Ent.* 58, p. 107; Schuurmans Stekhoven, 1926, *Treubia* vi, suppl., p. 281.

Chasmiia bicincta Enderlein, 1922, *Mitt. zool. Mus. Berlin* 10 (2), p. 344; (*nomen nudum*); 1925, *Mitt. zool. Mus. Berlin*, 11 (2), p. 331. New synonymy.

I am recognizing both the above species from descriptions, but the species is rather distinctive, in colour pattern, in structure of the antennae, and in length of wings.

♀. *Head.* Frons proportions 8:10:32, index 3, diverging. Callus spear-shaped, dark brown, filling the frons anteriorly. Tomentum of frons white, with some very short blackish hairs. Subcallus and extreme sides of parafacials, along eye margins, with yellowish grey tomentum, greater part of face and parafacials shining brown, rather swollen. Buccae with brown, then white tomentum, beard sparse, black. Antennae (Text-fig. 46): clear yellow basally, becoming darker on apical half of third segment, and blackish on following segments. Palpi slender, dark brown, with dark brown hairs.

Thorax. Mesonotum dark reddish brown, notopleural lobes and hind margin of scutum whitish; scutellum dark reddish brown, contrasting with white colour immediately in front of it. Sparse short black hairs, white hairs at sides, especially on notopleuron. Pleura dark brown with grey tomentum, except for a vertical brown stripe below the wing base. Hairs black on pteropleura, white on meso- and metapleura.

Abdomen. Shining dark brown, with a whitish transverse band, including hind margin of first segment and fore margin of second segment. Hind margin of second segment also whitish, but the extent of this is variable. Genitalia, which are just visible, are yellowish white. Hairs dark brown, white on white band. Venter similar, but the white transverse band broadened to include most of the first sternite.

Legs. Including coxae, black-brown with dark brown hairs, only knees very narrowly paler.

Wings. Pale at base, but yellow in costal cell and pale yellow-brown from base of discal cell to tip. Colour rather stronger along cross-veins. Anal cell open. R_4 without appendix.

Length. Body 8 mm.; wing 9 mm.

Enderlein's type material, in the Zoologisches Museum, Berlin, is said to be from Grat, 3,500 ft., 28.xi.1912; Lordberg, 8-10.xii.1912; Meanderburg, 3,200 ft., 17.viii.1912—three localities I have not been able to trace. The holotype of de Meijere's species, in *Natura Artis Magistra*, Amsterdam, is from Bougainville Mts., 1,600 ft., 1.vi.1910.

In the British Museum are two females, Cyclops Mts., Sabron, 2,000 ft., v.1936 (Cheesman); one female, Humboldt Bay Dt., Bewani Mts., 1,200 ft., vii.1937 (Stüber). In the Archbold Collection two females, Bernhard Camp, 15.xi.1938, 1,800-2,500 ft. (Olthof); mountain slope above Bernhard Camp, 2,200 ft., 25.iii.1939 (Toxopeus).

CHASMIELLA PAPOINUS.

Tabanus papouinus Walker, 1865, *J. Proc. Linn. Soc. Lond.*, viii, p. 108; Osten-Sacken, 1882, *Ann. Mus. civ. Genova*, 16, p. 418; Ricardo, 1913, *Nova Guinea*, 9, p. 401; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 298.

This is one of Walker's species described from a unique male, and so difficult to relate to a classification based largely on the structure of the female head. The male type is in the British Museum. The grey-dusted, cinereous pleura distinguish it from the rest of this group, and earlier authors have drawn attention to the way in which the small facets of the eye extend in a narrow strip along the hind margin, up to the vertex. Osten-Sacken (1882, p. 418) records a female of this species, from Sorong, in the Vogelkopf, with the remark: "M. Walker describes a male, nevertheless the description agrees tolerably well." Apart from this rather dubious identification no author seems to have recognized the species again, or described a female.

I have not seen a female, but in the material received from the South Australian Museum is a male from N. New Guinea, Mt. Gyifrie, sea-level to 100 ft., April, 1939 (Cheesman), which agrees closely with Walker's type except that the pale hairs of thorax and abdomen are yellowish rather than silvery. The Archbold Expedition also took a male at Hollandia, vii.1938, at sea-level (Toxopeus).

CHASMIELLA OCHROTHORAX.

Tabanus ochrothorax Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 444.

Tabanus brevisculus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 401, *nec* Walker, 1865.

Distinguished from the other species of this group by the much greater extent of the frontal callus (Text-fig. 45). The raised median ridge can still be distinguished, but almost the whole frons is bare and shining dark brown, only a small area in front of the median ocellus being faintly tomented. Third antennal segment shorter and broader, with a more prominent tooth.

♀. *Head.* Frons proportions 5:3:36, index $4\frac{1}{2}$. Frons (Text-fig. 45) almost entirely bare, shining dark brown, only a small area near the median ocellus being very sparsely tomented. Subcallus and face yellow, with yellow tomentum and hairs. Parafacials brownish, with dark brown hairs. Antennae (Text-fig. 45) yellow, segments beyond the

third reddish yellow, hairs mixed golden and dark brown. Third segment rather short and broad, with pronounced tooth. Palpi yellow, obscured on outer face by rather long, black hairs.

Thorax. Dorsum bright orange, with obscure dark median stripe extending on to scutellum; this can be seen in the paratype in the British Museum, though it is faint, and was not mentioned in the original description. In some other specimens it is more definite. Hairs on stripe mainly brown, laterally yellow. Pleura yellow, with yellow hairs.

Abdomen. Orange on first three tergites, following tergites blackish, lamella orange. Hairs golden on sides of first tergite and anterior side margins of second, otherwise mainly dark brown. Venter similar, with mainly golden hairs.

Legs. Coxae and femora orange, with mainly golden hairs. Tibiae and tarsi dark reddish brown, with black hairs.

Wings. Membrane faintly smoky, very narrowly browned at wing tip. Stigma yellow-brown.

The female holotype, from the Lorentz material, is in *Natura Artis Magistra*, Amsterdam, and other original specimens are in the Rijks Museum of Natural History, Leyden, the Buitenzorg Zoological Museum, and the British Museum. The British Museum has a paratype female from Heuvelbivak, 7-15.xi.09 (Lorentz), and a male from Bivakisland, xii.09; there is also a male from Alkmaar, 2.ii.10 (Lorentz), which Stekhoven made his male type, but I am not sure that it belongs to this species. I am inclined to associate it with *subhastata*, n. sp.

Also in the British Museum are: two females Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938; two females Cyclops Mts., Mt. Lina, 3,500 ft., iii.1936 (Cheesman). In the Archbold Collection are two females from Araucaria Camp, 2,500 ft., iii.1939 (Toxopeus). In the U.S. National Museum one female, Hollandia, April, 1945 (Malkin), two females Cyclops Mts., 1,000 ft. (Jean Laffoon).

There is a fair amount of variation in this series, but I think the variants come within the range of one species. The Japen Is. specimens have a very bright orange mesonotum, with orange hairs here and on the first abdominal segment, and no trace of median darkening. The mainland specimens have abundant short brown hairs on the mesonotum and first abdominal segment. There is variation, too, in the exact shape of the callus at the upper end, and in the extent of the tomentum visible there. The females in the Washington Collection have the callus strongly tapered from the base upwards.

CHASMIELLA SUBHASTATA, n. sp.

Distinguished from *ochrothorax* S.S. chiefly by the much shorter callus (Text-fig. 50), and perhaps only a form of it.

♀. *Head.* Frons proportions 7:8:45, index $5\frac{1}{2}$. Frons grey-dusted, callus shining brown, a long, bare area extending down from vertex. Hairs yellowish. Subcallus dull, tomented, pale yellowish, face and parafacials similar. Hairs brown below the eye, yellow elsewhere. Antennae (Text-fig. 50): first two segments yellow, third more reddish, terminal segments black. Hairs mostly yellow, some black. Palpi orange, slightly darker at tips, with mostly yellow hairs.

Thorax. Dorsum, including scutellum, yellow, obscurely brown in centre-line. Hairs mainly dark brown, golden hairs more numerous near margins. Pleura golden yellow, with golden hairs, no trace of a dark band.

Abdomen. First three tergites and anterior margin of fourth, orange; fourth, fifth and sixth tergites black; extreme tip of abdomen orange. Hairs dark brown, golden on sides and at tip of abdomen, and on hind margin of first tergite, which has a median triangle of yellow hairs. No yellow hairs along margins of other segments. Venter similar, with predominantly yellow hairs.

Legs. Femora yellow, tibiae and tarsi darker, or almost black. Coxae and middle and hind femora with longer golden hairs, rest of legs with shorter black hairs.

Wings. Membrane faintly yellowish, not distinctly smoky anywhere. Stigma clear yellow-brown.

Length. Body 7 mm.; wing 9 mm.

Holotype female and eight female paratypes, Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938; five females Waigeu, Camp Nok, 2,500 ft., iv.1938; one female W. New Guinea, Mt. Nomo, S. of Mt. Bougainville, 700 ft., ii.1936, one female, Papua, Mafulu, 4,000 ft., i.1934 (all Cheesman)—all the above in the British Museum.

In the Archbold Collection are two females, Araucaria Camp, 2,500 ft., 7.iii.1939 (Toxopeus). In the School of Public Health and Tropical Medicine, Sydney, one female, Zoutbron, 20-30.vi.1910 (? coll.). In the South Australian Museum, three females, Mt. Lucreu, 2,000 ft., Jan., 1939; one female, Torricelli Mts., 800 ft., Jan., 1939 (Cheesman).

Some specimens have the darker colour of the mesonotum, abdomen and tibiae less well developed, or almost absent. This variation does not seem to be correlated with locality.

CHASMIELLA PARVA, n. sp.

Again very similar to *ochrothorax* and to *subhastata*, and perhaps no more than a form. The callus is narrower and paler, and set on a narrower frons, further removed from the eye margins (Text-fig. 47). Stigma dark brown, and palpi blackish with black hairs.

♀. *Head.* Frons proportions 8:8:45, index $5\frac{1}{2}$. Frons brownish grey dusted, callus yellow-brown (Text-fig. 47), more slender in outline, and not completely filling frons at its lower end. Barer area at vertex paler and less prominent than in *subhastata*, but median ocellus very well developed. Subcallus and face entirely tomented reddish brown; parafacials with brown tomentum and dark brown hairs. Antennae (Text-fig. 47): third segment with less prominent tooth than in *subhastata*, first two segments yellow, with mostly black, and some yellow hairs, third segment more reddish, rest black. Palpi: first segment yellow, second segment blackish, both with rather dense black hairs.

Thorax. Dorsum, including scutellum, reddish yellow, hairs black on disc, golden at sides and on hind margin. Pleura yellow, with golden hairs.

Abdomen. First three and a half segments orange, the rest black. Anal lamellae orange. Hairs black, golden on side margins and in median triangle on first segment. Venter similar, with golden hairs.

Legs. Coxae yellow, with mainly yellow hairs. Fore femora reddish brown, with mainly black hairs, middle and hind femora yellow with mainly yellow hairs. Tibiae and tarsi reddish brown with black hairs.

Wings. Membrane faintly smoky, distinctly browned along margin, from stigma to wing tip. Stigma dark brown.

Length. Body 8 mm.; wing 9 mm.

Holotype female and six female paratypes, Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938 (Cheesman). A single female from Milne Bay, Feb. 1943 (Mackerras), in the material from Mr. Lee, seems to represent a form of this species, in which the sides of the facial tubercle (i.e., not the parafacials) are bare and shining brown, and the stem of the proboscis appears to be excessively long and thin. I suspect this latter is a distortion. It looks as if the labium had originally been broken off and had been replaced by neatly impaling it on the tip of the stylets.

CHASMIELLA FULGIDUS.

Tabanus fulgidus Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 402; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 385.

A tiny species with orange, black-tipped antennae; a short, broad, spear-shaped callus; shining face; yellow-brown thorax with blackish scutellum and blackish vertical pleural band; abdomen red-brown, darkened apically; legs dark.

♀. *Head.* Frons proportions 8:10:35, index $3\frac{1}{2}$. Frons grey-dusted, callus shining brown (Text-fig. 23), a longish bare area on the site of the ocellar callus. Hairs pale yellowish. Subcallus dull, tomented, pale yellowish. Face shining, transparent yellow-

brown, bare patch extending a little on to parafacials, rest of parafacials and epistoma with white tomentum, except for a vertical brown band immediately beside the base of the proboscis. Hairs and bristles pale, a few brown ones below the eye. Antennae (Text-fig. 23): orange with brown and yellow hairs, last four flagellar segments black. Palpi blackish on outer side with black hairs, inner face yellowish, bare.

Thorax. Dorsum yellow-brown, rather shining, noticeably white-dusted on humeri, notopleural lobes, and hind margin of scutum. Scutellum blackish, contrasting markedly with scutum. Hairs mixed golden and dark brown, predominantly brown on scutellum. Pleura more whitish than dorsum, except for a broad black band running vertically down from the wing-root. Hairs yellowish.

Abdomen. First and second tergites, and anterior margin of third tergite, yellow, following tergites dark brown, all with brown hairs on disc, and yellow hairs on hind margin, especially in the middle line. Venter similar.

Legs. Dark brown, with hairs same colour. Fore coxae similar, with some yellow hair, middle and hind coxae coloured like pleura, with yellow hair.

Wings. Very faintly smoky along fore border and on basal portion of radial sector. Stigma dark brown.

Length. Body 6-7 mm.; wing 9 mm.

In the two female paratypes the rather distinctive colour-pattern is somewhat faded, and the above description is drawn up from the Japen series, in which the pattern is accentuated. This is particularly noticeable in the dark tips of the antennae, the blackish scutellum, and the more sharply-defined boundary to the light and dark areas of the abdomen. It may be that the island specimens are slightly atypical in this respect.

Holotype female in the *Natura Artis Magistra* Collection is from Heuval Bivak (Lorentz). In the British Museum are two paratypes from the same locality, and 19 females from Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938 (Cheesman).

CHASMIELLA RAFFRAYI.

Tabanus raffrayi Bigot, 1892, *Mém. Soc. zool. France*, v. p. 690; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 402; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 291.

Previous authors have seen only the holotype female, which is very badly preserved. The following description is taken from a modern specimen, which I have compared with the type.

♀. *Head.* Frons proportions 8:9:53, index 6. Callus (Text-figs. 25, 48), elongate, tapering, black-brown. Tomentum of frons dark yellow-brown, with yellow hairs. Subcallus with yellow-brown tomentum, face more reddish, hairs brownish. Antennae (Text-figs. 25, 48): first two segments reddish yellow; third segment basally reddish, apically blackish; terminal segments black; from third segment onwards unusually pubescent. Palpi dark brown with black hairs.

Thorax. Mesonotum translucent dark brown, more yellowish laterally and anteriorly, humeri whitish. Hairs short, black. Pleura with a dark brown, brown-haired band running vertically in front of the wing, rest of pleura greyish with white hairs.

Abdomen. Dark brown, slightly paler anteriorly, segments narrowly pale, this margin more pronounced on the first two segments. Hairs black, some white hairs on segmentations. The type and the Mafulu specimen show median triangles, which are barely indicated in the Japen specimens. Venter black-brown, paler basally, with segmentations indistinctly and very narrowly paler, hairs all black (cf. Stekhoven's description).

Legs. Black-brown or obscurely reddish, with black hairs.

Wings. Clear, very slightly yellowed in costal cell and first half of first basal cell. Anal cell just closed or slightly open. Stigma relatively large, dark brown.

Length. Body 7 mm.; wing 9 mm.

All the specimens known to me are in the British Museum. Bigot's female holotype is from "New Guinea"; one female, Papua, Mafulu, 4,000 ft., 1.1934; 16 females, Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938; two females Waifor and Mt. Nok, 2,500 ft., iv.1938 (Cheesman).

CHASMIELLA BREVIUSCULUS.

Tabanus brevisculus Walker, 1865, *J. Proc. Linn. Soc. Lond.*, viii, p. 109; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 401; Enderlein, 1922, *Mitt. zool. Mus. Berlin*, 10 (2), p. 344; 1925, *Mitt. zool. Mus. Berlin*, 11 (2), p. 331; Schuurmans Stekhoven, 1926, *Treubia* vi, suppl., p. 451. Genotype of *Chasmiella* End., 1922, by original designation.

Distinguished from *fulgidus* Ric. by its larger size, more spindle-like callus and tomented face.

♀. *Head*. Frons proportions 9:8:53, index $6\frac{1}{2}$, parallel. Callus slender, extending half-way towards vertex and occupying only half width of frons at antennae. Rest of face tomented, no distinct bare area at vertex. Median ocellus present. Hairs yellow. Subcallus and face with yellowish brown tomentum, parafacials slightly more blackish, with dark brown hairs. Antennae (Text-fig. 49): first three segments yellow, following segments darker; third segment rather elongate with well-marked tooth; hairs on first two segments chiefly black. Palpi dark reddish brown, with mainly black hairs on both segments.

Thorax. Dorsum brownish yellow with mixed yellow and black hairs in about equal numbers. Pleura yellow, a broad vertical brown stripe through mesopleuron and adjoining parts of pteropleuron and sternopleuron. Hairs yellow, except on upper part of mesopleuron and notopleural lobe.

Abdomen. First three tergites yellow-brown, others dark brown, boundary of light and dark areas rather obscure. Hairs chiefly dark brown, yellow along hind margins and sides of first segment, and on lateral hind margins of other segments. Venter similar, with brown hairs on discs of segments and yellow hairs on hind margins.

Legs. Coxae brownish yellow, with predominantly yellow hairs, some black. All femora dark reddish brown, with mainly black hairs. Fore tibiae and fore and middle tarsi similar; middle and hind tibiae and hind tarsi more yellowish, also with black hairs.

Wings. Membrane distinctly smoky, only a trace of dark brown at extreme wing tip. Stigma yellow-brown. Tegulae, which in other species of this group have rather inconspicuous yellow hair, here have black hair.

Length. Body 9 mm.; wing 10 mm.

Male holotype in the British Museum is labelled "New Guinea" (Wallace). Miss Ricardo associated with it a number of specimens taken by the Lorentz Expedition, but Stekhoven correctly described these as his new species *ochrothorax*.

In the U.S. National Museum collection is a single male from Cyclops Mts., 1,000 ft., March, 1945 (Jean Laffoon), which agrees perfectly with Walker's type. There is a clear vertical brown band on the pleura, emphasized by long brown hairs on the meso- and sternopleura and the notopleural lobe. This distinguishes the species from any other in the genus, except *fulgidus* Ric., from which it differs in the dull tomented face, paler legs, paler stigma. It looks, in fact, bigger and less strongly patterned than *fulgidus*. The fresh specimen shows that the mesonotum—including scutellum—is clothed with rather long, silky, dark brown hairs, which seem to stop abruptly at the level of the transverse suture, leaving the fore margin bare.

I have associated with these males two females in the Archbold collection, from Araucaria Camp, 2,500 ft., 2.iii.1939 (Toxopeus), which are the basis for the description given above.

Enderlein (1922, 1925) erected the genus *Chasmiella* for this species, the subfamily Chasmiinae being characterized by the open anal cell. He cannot have seen Walker's type, which has the anal cell closed and stalked in both wings. His few remarks in explanation of the genus imply that he had specimens of some sort before him, since he refers to the relative length of the antennal segments, and says that exceptionally

the anal cell may be closed on the wing margin. It is a pity that his use of the name *breviusculus* is so dubious, because this group of tiny Tabaninae is distinctive in general appearance, and it should be possible eventually to define it by more reliable characters. The anal cell is open in some specimens before me, but is closed in the majority.

CHASMIELLA FASCIATA, n. sp.

One of two species that are readily recognized by their squat shape and yellow-and-black banded appearance, the black-brown scutellum being very prominent. The present species is further recognized by the banded pleura and black fore femora. The only female specimen is greasy, so, where necessary, reference is made to the male for details of coloration.

♀. *Head.* Frons proportions 11:11:54, index 5, parallel. Callus light brown, tapering (Text-fig. 52). Tomentum of frons golden, black at vertex. Subcallus and facial area golden, a little more blackish on parafacials, a little reddish in middle of face. Beard sparse, black. Antennae (Text-fig. 52): first two segments bright yellow, with black hairs at sides, yellow hairs dorsally and ventrally. Third segment bright orange, terminal segments brown. Palpi orange, with mainly black hairs. Proboscis brown.

Thorax. Mesonotum yellow, with three broad, black-brown, longitudinal stripes; middle one broadest anteriorly, tapering towards scutellum, lateral stripes straight on inner margin, convex on outer. Scutellum entirely black-brown, contrasting strongly with scutum. Short black hairs more numerous on dark stripes, yellow hairs at sides and posteriorly, long black hairs all over scutellum. Pleura yellow, with yellow hairs, but immediately below wing base the anterior half of the mesopleuron is black-brown, with black hairs.

Abdomen. Dorsum black-brown, first two tergites partly or wholly yellow. Hairs mainly black, hind margin of first segment with pale yellow hairs and a yellowish median triangle, other segments with white hairs in a median triangle, and white hairs on the side margins; terminal segments with more numerous white hairs. Venter similar, but without white-haired segmentations and triangles.

Legs. Coxae yellow with pale yellow hairs. Legs otherwise mainly black-brown with black hairs, tibiae of middle and hind legs paler, with dark tips.

Wings. Hyaline with pale yellow stigma.

Length. Body 8 mm.; wing 10 mm.

♂. Closely resembles female, except for the usual secondary sexual differences, chiefly the shorter palpi and longer clothing hairs, which give the body a more woolly appearance.

Holotype female, three male paratypes, Araucaria Camp, 2,500 ft., 18-31.iii.1938 (Toxopeus) are in the Archbold collection. In the British Museum are one male and one female (headless) paratypes from 14° E., 3° 10' S., 900-1,800 ft. (Stüber). In the U.S. National Museum is one female paratype from Nadzab, Markham R. valley, July, 1944 (Krombein).

CHASMIELLA PARVACALLOSA, n. sp.

Allied to *fasciata*, but easily distinguished from it by the form of the callus, the unbanded pleura, the yellow fore femora and the more definitely banded abdomen, especially the clear-cut band on the second segment.

♀. *Head.* Frons proportions 12:12:50, index 4, parallel. Callus (Text-fig. 51) very short, oblong, far removed from the eye margins, pale yellow. Frons bone-yellow, with white tomentum and yellowish hairs. Subcallus and facial area similar, but with black hairs in beard. Antennae (Text-fig. 51): first segment bone-yellow with yellow hairs; second segment light brown with black hairs; third segment bright orange, with well-defined tooth tipped with a few black hairs; terminal segments brown. Palpi white, with black hairs. Proboscis whitish at base, a little brown towards tip.

Thorax. Mesonotum yellow, with stripes of the sort described in *fasciata*, but much more faintly indicated. Scutellum entirely black-brown. Pleura entirely yellow, with yellow hairs, no vertical dark band.

Abdomen. First segment and basal quarter of second tergite yellow, extreme hind margins of other tergites whitish, rest of abdomen black. Boundaries of colour bands more sharply defined than in *fasciata*. Hairs black, rather long, recumbent, pale yellow on yellow bands, and a thick fringe of white hairs along each hind margin. Pattern extends to very edge of tergites, no lateral tufts. Venter black, with black hairs, first three segments yellowish.

Legs. Coxae and femora yellow, tip of fore femur and apical third of hind femur blackish. Hairs yellow on coxae and most of femora, black on blackish areas and on most of hind femur. Tibiae and tarsi black with black hairs.

Wings. Clear hyaline, with yellow stigma. Anal cell closed on wing margin.

Length. Body 10 mm.; wing 10 mm.

In the British Museum are holotype female and one female paratype from Papua, Kokoda, 1,200 ft., viii.1933 (Cheesman); two female paratypes, 140° E., 3° 10' S., 900-1,800 ft., Jan., 1937-8 (Stüber).

Genus JAPENOIDES, gen. n.

Frons, subcallus, parafacials and face all swollen, bare and shining dark brown. Only antennal sockets, buccae and extreme edge of parafacials along eye margins are tomented. Frons a bulging ridge, diverging towards antennae, with a well-defined, prominent ocellar tubercule, but no ocelli. Antennae: first segment proportionately large, but not inflated nor of markedly unusual shape. Proboscis with fleshy labella occupying about half total length. Wing heavily browned, anal cell closed, with a short stalk, R_4 with short appendix.

One species from the island of Japen, hereby designated as genotype.

JAPENOIDES CHEESMANI, n. sp.

A smallish, slender, dark species, with blackish wings.

♀. *Head.* Frons proportions 7:12:35, index 3, diverging towards antennae. Frons bare, shining dark brown. Subcallus bare, shining, a little lighter in colour than the frons, with brown tomentum around sockets of antennae. Face and parafacials a highly polished mahogany-brown, parafacials with dark brown hairs. Buccae with brown tomentum and dark brown or black hairs. Antennae: first segment black-brown with black hairs, second segment yellow-brown with black hairs, third segment bright orange, terminal segments blackish. Palpi slender, dark-brown, with dark brown hairs.

Thorax. Mesonotum grey-black, scutellum and postalar calli a little reddish, with fine black hairs and numerous silky yellow ones. Pleura grey-black with mainly yellow hairs, a few black ones on mesopleuron.

Abdomen. Dorsum grey-black, more brownish towards apex, segmentations very narrowly paler. Some black hairs, but long, recumbent, silky yellow hairs are prominent on all segments. Lateral margins with a yellow fringe. Venter black-brown, segmentations faintly paler, hairs mainly black, yellow only on segmentations.

Legs. Black or black-brown, with black hairs. Fore tibiae narrowly pale at base, middle and hind tibiae and first tarsal segments brown, black-tipped.

Wings. Brown, more deeply coloured on fore border and along all main veins. Stigma dark brown. Anal cell closed, with short stalk. R_4 with short appendix.

Length. Body 9 mm.; wing 9 mm.

Holotype female and 24 female paratypes from Japen Island, Camp 2, Mt. Eiori, 2,000 ft., x.1931 (Cheesman). I take pleasure in naming this species after Miss L. E. Cheesman, the distinguished explorer, whose fine collections from hitherto inaccessible parts of the New Guinea area are providing so much valuable data about this region.

Genus CYDISTOMYIA.

Cydistomyia Taylor, 1919, PROC. LINN. SOC. N.S.W., 44 (1), p. 47. Genotype: *C. doddi* Taylor, 1919, by original designation (= *T. albithorax* Ric., 1913).

It is usual in classifying the Tabaninae to separate off all the readily-definable units, leaving the miscellaneous residue under the generic name 'Tabanus'. In the New Guinea fauna, however, the name *Tabanus* is most appropriately applied to the relatively well-defined group with hairy subepaulets. The miscellaneous residue in this fauna has bare subepaulets. As a comprehensive name for this group I have used the name *Cydistomyia*, the genotype of which is a New Guinea species.

It is certain that the species I have included under this name are not a natural group, and will ultimately be distributed into several genera. Some will be referred to Oriental genera, some to Australasian genera, and some, perhaps, be indigenous to New Guinea, but until the genera of these bigger areas are better-defined this cannot be done. The genotype, *C. albithorax* Ric. (*doddi* Tayl.), stands apart from the rest. Ferguson (1926, p. 301) says of it: "Although unlike any other Australian species in general habitus, it conforms well with some extra-limital species, such as *T. sharpei*" (= *insignis* Lw.), "though there are, of course, specific differences". This is not my impression. *T. sharpei*, an African species, has hairy subepaulets, spiracles with a well-defined lip, and a broader face, with the palpi further apart. I do not think there is more than a superficial resemblance.

KEY TO THE NEW GUINEA SPECIES OF CYDISTOMYIA.

1. Abdomen very pointed, showing seven very distinct, tapering segments, the eighth sternite and lamellae protruding freely at tip. A small, dark brown and yellow species *lamellata*, n. sp.
- Abdomen not so constructed 2
2. Frons without a shining callus 3
- Frons with distinct shining callus 5
3. Grey species, without abdominal pattern *caesius* Wlk.
- Yellow-brown species with median triangles 4
4. Pleural hairs mainly white, third antennal segment shorter; palpi more slender *pseudimmatura*, n. sp.
- Pleural hairs mainly brown, third antennal segment longer; palpi very short and plump *immatura*, n. sp.
5. Subcallus bare and shining. A strikingly-patterned species, with dull yellow thorax, dark brown abdomen; wings dark brown, with pale tip. Pleura, venter and legs brown *imitans*, n. sp.
- Subcallus covered with tomentum 6
6. A very distinctive species. Mesonotum yellowish grey, with prominent silky yellow hairs all over disc. First four abdominal segments bright orange, with orange hairs; following segments black, with black hairs. Antennae orange, first segment rather long. Palpi orange, very slender. Frons diverging, ocellar tubercle present, callus a swollen, diverging ridge (Text-fig. 55). Wings partly browned, R_4 with long appendix *festiva*, n. sp.
- Without this striking colour and pattern 7
7. Species with a distinct colour-pattern of triangles or bands on abdomen, sometimes on thorax as well 8
- Yellow-brown, yellow or grey species, sometimes dark in part, but without clear-cut abdominal pattern 16
8. Dark brown species, thorax with a conspicuous pair of crescentic pale bands immediately before scutellum. Abdomen with a single median row of separated pale triangles, and with extreme side margins pale on some segments. Body plump, wings long, with half their length beyond tip of abdomen. Ocelli more or less well developed *albithorax* Ric.
- Without conspicuous pale crescents on thorax. Either more elongate or, if rather plump, then wings do not extend very far beyond tip of abdomen 9
9. Thorax as well as abdomen blackish brown, with white transverse bands. No median or lateral triangles on abdomen (♀). Pleura white or greyish, with vertical dark brown band below wing base. First antennal segment rather long, but not cylindrical in side view (Text-fig. 56). Male with first two abdominal segments yellow .. *dimorpha*, n. sp.
- Thorax without these transverse bands 10
10. Middle-sized (15 mm.), grey and black species, abdomen with one median row of very distinct, separated, rounded pale spots; base of second segment also pale. Like *T. semicircularis*. Thorax with pale side margins, and two pale longitudinal stripes. Subcallus dark brown, contrasting with face 11

- Triangles, if present, angular and smaller, much less conspicuous. Species dark brown and yellow in colour 12
11. Larger species (13 mm.). Frons broader, index 3; antennae as in Text-figure 68 *heydoni*, n. sp.
 Smaller species (10 mm.). Frons narrower, index 3½. Antennae as in Text-figure 66 *misisimensis*, n. sp.
12. Antennae stouter, third segment and flagellum relatively shorter and broader (Text-fig. 65). Dark brown or black species, scutellum and segmentations white, triangles barely indicated. Anterior tentorial pits deep, circular. Callus elongate spear-shaped *aluensis*, n. sp.
 Antennae slender, third segment relatively longer (Text-figs. 24, 64, 69, 70). Light brownish or blackish species, scutellum somewhat paler. Abdomen with very thin, angular, but distinct triangles. Callus otherwise shaped. Anterior tentorial pits shallow, slit-like 13
13. Wings distinctly darkened along fore border and at apex. Mesonotum rather bare, yellow-brown, with white scutellum, contrasting with darker abdomen, which has distinct median and extreme lateral triangles. Terminal segments of antenna not contrasting in colour with third segment *laetus* de Meij.
 Wings little or not at all darkened. Mesonotum dark brown or blackish, with greenish scaly hairs as well as black hairs; scutellum not contrasting. Abdomen may be rather lighter in colour than thorax, at least basally 14
14. Femora shining dark brown or black, tibiae yellow at base, black apically. Costal cell yellow, anterior border a little browned *nigerrima*, n. sp.
 Femora not so; at most a little greyish 15
15. Smaller species (10 mm.). Callus with a distinct neck between lower portion and linear extension (Text-fig. 64). Terminal antennal segments darker than the third segment *immigrans*, n. sp.
 Larger species (13 mm.). Callus smoothly narrowed into linear extension (Text-fig. 69). Terminal antennal segments not darker than the third segment *inopinata*, n. sp.
16. Frons narrow, index 7 or more, strongly tapering 17
 Frons broader, index 6 or less, parallel, or not strongly tapering 18
17. Frons exceptionally narrow, tapering towards antennae, but narrowest in middle, callus almost linear (Text-fig. 22) [solomonensis Ric.]
 Frons tapering evenly towards antennae, not narrowest in middle. Callus strongly expanded at its lower end (Text-fig. 62) *nokensis*, n. sp.
18. A brown species, with bicoloured thorax: scutum divided at transverse suture into a greyish yellow anterior half, and a dark brown posterior half. Pleura divided horizontally, mesopleuron and entire upper half being yellow, sternopleuron and lower half brown *bisecta*, n. sp.
 Thorax not so divided 19
19. Face bare and shining. A deep red-brown species, with dark brown and red-brown hair. Wing uniformly browned; R₄ quite rectangular at base, with moderately long appendix *oudella*, n. sp.
 Face tomentose 20
20. Dark brown or blackish species, with predominantly dark brown hair, thick and bushy on all parts of body, giving the whole insect a blackish appearance. Thorax (greasy) very black, abdomen with entirely black hairs, no reddish or yellowish ones even at sides *crepuscularis*, n. sp.
 Yellow or reddish yellow species; if brown hairs are present, they are not dense enough to obscure ground-colour, and do not give whole insect a blackish appearance. Abdomen with orange or reddish hairs, at any rate at sides 21
21. Larger (13 mm.) species, reddish, with brown or black hairs on palpi and legs, and sometimes on beard. Wings may be stained brown *lorentzi* Ric.
 Smaller (11 mm.) species, yellow, with predominantly yellow hairs, including palpi, beard and legs *sol* S.S.

CYDISTOMYIA ALBITHORAX.

Tabanus albithorax Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 391; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., pp. 338-341.

Cydistomyia doddi Taylor, 1919, Proc. Linn. Soc. N.S.W., 44 (1), p. 47; Ferguson, 1926, *Bull. ent. Res.*, 16 (4), p. 301.

C. doddi was described from a specimen submitted by Mr. F. P. Dodd and alleged to be from Kuranda, Queensland. In 1940 Mr. Taylor wrote to me that the species had never again been found on the mainland of Australia, and that he had come to the conclusion that there had been an error of locality. Mr. Dodd collected in Papua, as well as in Queensland, and the species might well belong to the New Guinea fauna. Mr. Taylor added that this species, "or something very near it", was well represented in Miss Cheesman's material from Papua.

When the collections came back to me I easily recognized the species in question, and found that Mr. Taylor had labelled one specimen as *C. doddi*. The type of *T. albithorax* Ric. is in the British Museum, and the two are undoubtedly the same species. In the MS. I saw recently Mr. G. H. Hardy stated that the mainland specimens, including the type, were missing, but that the species was represented in the Queensland Museum by New Guinea specimens.

It is remarkable that no author has emphasized the crescentic transverse markings of the thorax, which are such a distinctive feature of this species. It is a short, stoutly-built species, chocolate-brown, the thorax adorned with yellow markings as follows: on the anterior half, two longitudinal stripes and two oblique stripes on the transverse suture, at the sides; on the posterior half a pair of crescentic marks on the hind margin of the scutum, immediately before the scutellum. Abdomen with distinct, isolated, median pale triangles, and extreme lateral angles pale. Wings very long, half their length extending beyond tip of abdomen.

♀. *Head*. Frons proportions 16:18:63, index $3\frac{1}{2}$. The vestiges of three ocelli are present as tiny pale spots, though they do not protrude above the surface. Bare callus as in Text-fig. 20, though the whole frons bulges forwards. Tomentum brown, narrowly white on eye margins. Subcallus, parafacials and face with thick white tomentum and white hairs. Antennae (Text-fig. 20) reddish brown, first two segments with black hairs above and yellow hairs below. Palpi slender pointed, brown with mostly brown hairs, but with long, white, silky hairs on first segment and base of second. Proboscis a little longer than palpi, labella about half total length.

Thorax. Chocolate-brown, more yellowish on anterior half. Humeri orange, notopleural lobes yellow. Yellow bands also on each lateral third of transverse suture, connecting with a pair of longitudinal yellow lines on prescutum. Hind margin of scutum broadly pale yellow, forming a pair of very noticeable crescent-shaped markings. Scutellum entirely chocolate-brown. Pleura orange or yellow in ground-colour, with thick white tomentum. Hairs of thorax black on brown areas, yellow on yellow areas, white on white areas.

Abdomen. Dorsally chocolate-brown, with black hairs. A single median row of very clear-cut yellow median triangles, with yellow hair; that on second segment is largest, equilateral, and not more than half length of tergite, following ones broad but low. Extreme hind-angles yellow, especially on first to third segments. Venter entirely covered in whitish tomentum, with pale yellowish hairs.

Legs. Reddish brown, tarsi and tips of tibiae more blackish. Long hairs of femora white, other hairs of legs black.

Wings. Clear except for yellow-brown stigma. No appendix.

Length. Body 10 mm.; wing 12 mm.

♂. Similar.

In the British Museum: Holotype female, Iwaka R., 1911 (Wollaston); three females, Heuvelbivak, 600 ft., 7-15.xi.09 (Lorentz); paratypes, five females, Papua, Mt. Tafa, 8,500 ft., iii.1934; four females, one male, Mafulu, 4,000 ft., i.1934; six females, Mondo, 5,000 ft., ii.1934; one female, Yule Is., Matsika, iii.1934; one female, W. New Guinea, Mt. Nomo, S. of Mt. Bougainville, 700 ft., ii.1936 (all coll. by Miss Cheesman).

In the Archbold collection: four females, Araucaria Camp, 2,400 ft., 15-22.iii.1939 (Toxopeus); five females, Bernhard Camp, 1,800-2,400 ft., 5.xi.1938 (Oltorf); one female same locality, 300 ft., 2.iv.1939 (Toxopeus), three females Lower Mist Camp, 4,400 ft., 30.i-2.ii.1939 (Toxopeus); one female, Sigi Camp, 4,000 ft., 22.ii.1939 (Toxopeus); one female, Rattan Camp, 3,600 ft., 5.iii.1939 (Toxopeus).

In the School of Public Health and Tropical Medicine, Sydney, one female, Hoofd-bivak, 750 ft., Dat. ix (v. Leeuwen). In the S. Australian Museum, one female, N. New Guinea, Mt. Lucreu, 2,000 ft., Jan., 1939 (Cheesman). In the Harvard collection, 1 female, Papua, Morobe Dt., Mt. Misim (Stevens).

This species is easily recognized by its general appearance and pattern, but is very variable in detail, especially in the colour of hairs of head, pleura and legs. Stekhoven (1926) named three varieties based on such differences. In my series from Papua,

Mafulu, the legs are very black and the mesopleuron has a bright yellow tuft like that on the notopleural lobe, but I do not find any consistency, except among specimens collected on the same day, and in the same place.

CYDISTOMYIA LAMELLATA, n. sp.

A small, clearly-patterned, brown and yellow species, quite like *lactus* de Meij. The protrusion of the anal lamellae looks like an artefact due to drying of the specimen, but it is present in all the specimens I have seen. If it represents a real difference of structure it would call for a new genus.

♀ *Head*. Frons proportions 10:10:40, index 4, parallel. Callus short, rounded, with moderate linear extension (Text-fig. 54). Vertex has a large brown triangle with strong black hairs, and a slight ocellar tubercule. Otherwise tomentum of face, subcallus, and entire facial area is yellow (there is a small brown patch just above rostrum, in middle of face). Hairs, including parafacial hairs and beard, dark brown. Antennae (Text-fig. 54): first two segments brown with black hairs, third segment bright orange, following segments black. Palpi brown with dark brown hairs.

Thorax. Mesonotum dark brown, yellowish along longitudinal and transverse sutures, and along sides, and round margin of scutellum. Pleura yellow-brown, a darker patch on sternopleuron, extending on to lower mesopleuron, whitish on some sutures; hairs light brown.

Abdomen. Seven segments are clearly visible, the posterior ones tapering; a narrow ring of the eighth tergite can be seen and beyond this the anal lamellae protrude for a distance at least equal to the breadth of the seventh tergite. Abdomen very pointed in appearance. Dorsum dark brown, first five or six segments with a yellowish white triangle in each hind angle and a yellowish white median triangle. Hairs black on darker areas, pale on pale areas. Venter dark brown with white segmentations, which are continued from the white lateral triangles of the tergites. Eighth sternite protruding by more than the breadth of the seventh sternite.

Legs. Dark brown, with black hairs, forelegs usually more blackish than others.

Wings. Relatively long. Hyaline, but with brown staining along most of main veins, especially marked along costa around wing tip and at tips of radial veins.

Length. Body 9 mm.; wing 10 mm.

In the British Museum are the holotype female and three female paratypes from Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938 (Cheesman); one female paratype, Japen Is., Seroei, Camp 1, Mt. Baduri, Ajam Range, 1,000 ft., 8.ix.1938 (Cheesman).

In the Archbold collection, the following paratypes: two females, Rattan Camp, 3,600 ft., ii.1939 (Toxopeus); one female, Mist Camp, 5,500 ft., 9.i.1939 (Toxopeus).

CYDISTOMYIA CAESIUS.

Tabanus caesius Walker, 1848, *List. Dipt. Brit. Mus.*, 1, p. 180; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 419.

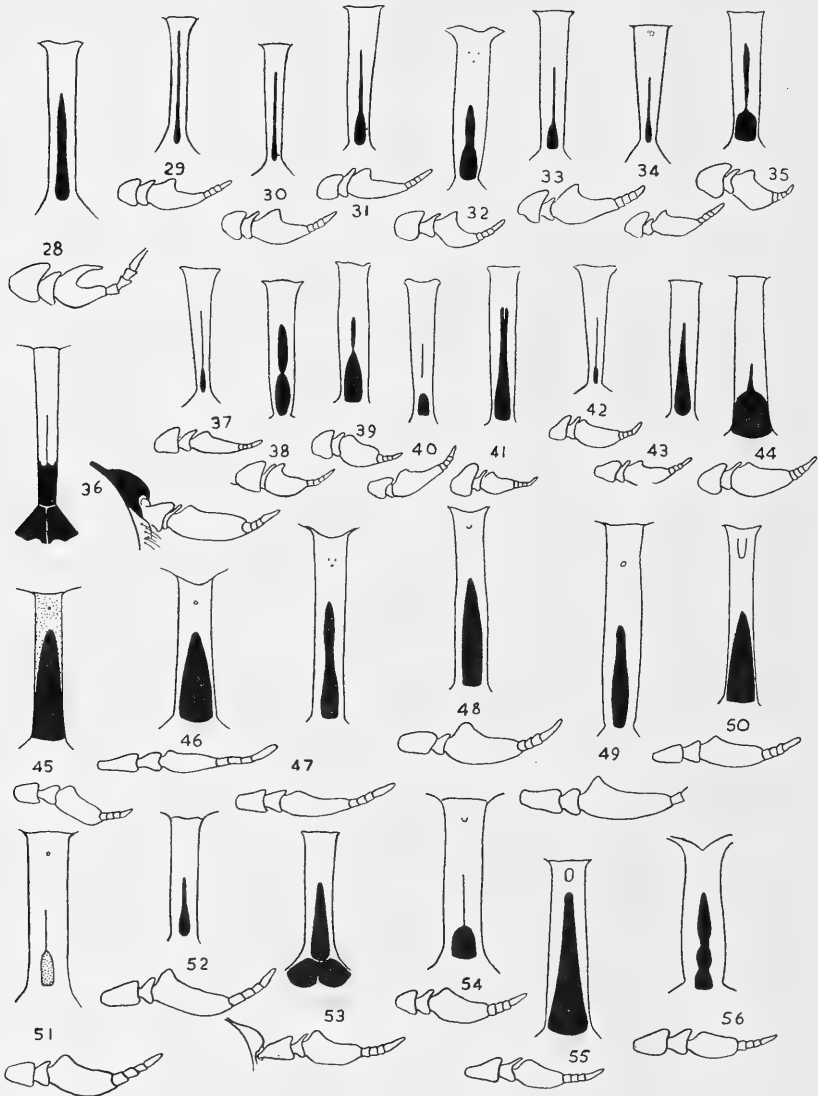
Tabanus leucopierus Wulp, 1868, *Tijdschr. v. Ent.*, 11, p. 98; Ferguson and Hill, 1922, *Proc. Linn. Soc. N.S.W.*, 57 (3), p. 254.

A middle-sized, pale grey species, without abdominal pattern, and with a broad, diverging frons with no frontal callus. Rubbing may produce an irregular bare area on the frons, but the raised ridge which is the basis of a true callus is absent in the type specimen. There is a faint trace of such a swelling, in an inverted heart-shape, in the second specimen in the British Museum.

♀ *Head*. Frons proportions 20:25:60, index 2½. Vertex deeply grooved. No frontal callus. Tomentum of entire head white. Frons almost evenly covered with short, curved, black hairs, each arising from a small black socket. Facial hairs and beard white. Antennae: first two segments yellow with some black hairs, but mainly white hairs. Third segment missing in both the available specimens, but Wulp says it is slightly excavated dorsally. Palpi long and slender, white, with white hairs. Proboscis yellow, labella about one-third of total length.

Thorax. Mesonotum grey, slightly reddish posteriorly, humeri and notopleural lobes yellowish. Clothed with fine black hairs and silky white ones. Pleura grey, with white hairs.

Abdomen. Dorsum grey with pale segmentations. Hairs are mingled black and white, with more pale hairs on segmentations, becoming longer towards rear. Venter similar, with entirely pale hairs.



Text-figures 28-56.

Figs. 28-56. Frons and antenna of female: 28, *T. denticulatus* Ric.; 29, *T. flavipennis* Ric.; 30, *T. cinnamomeus* Dol.; 31, *T. recusans* Wlk.; 32, *T. flammeus* S.S.; 33, *T. stuberi*, n. sp.; 34, *T. opalescens* S.S.; 35, *T. lenticulatus*, n. sp.; 36, *T. ceylonicus* Schin.; 37, *T. vanleeuweni*, n. sp.; 38, *T. productus*, n. sp.; 39, *T. truncatus*, n. sp.; 40, *T. patriarchus*, n. sp.; 41, *T. infuscatus*, n. sp.; 42, *T. approximatus*, n. sp.; 43, *T. daruensis*, n. sp.; 44, *T. angustilineatus*, n. sp.; 45, *Ch. ochrothorax* S.S.; 46, *Ch. basifasciata* de Meij.; 47, *Ch. parva*, n. sp.; 48, *Ch. raffrayi* Big. (modern specimens); 49, *Ch. brevisculus* Wlk.; 50, *Ch. subhastata*, n. sp.; 51, *Ch. parvicallosa*, n. sp.; 52, *Ch. fasciata*, n. sp.; 53, *Cyd. imitans*, n. sp.; 54, *Cyd. lamellata*, n. sp.; 55, *Cyd. festiva*, n. sp.; 56, *Cyd. dimorpha*, n. sp.

Legs. Yellow, femora a little greyish. Hairs pale on femora and underside of tibiae, black elsewhere.

Wings. Clear hyaline, without any colouring and with hardly a distinct stigma; veins yellow. R_1 with long appendix.

Length. Body 12 mm.; wing 11 mm.

Walker's type is from an unknown locality ("bought at Mr. Children's Sale"), but is clearly conspecific with a second specimen in the British Museum from New Guinea, 1901 (Kühn). Wulp's type is in the Rijksmuseum of Natural History, Leyden, and was collected in the Aroe Is. by Rosenberg. The species also occurs in the Northern Territory of Australia.

The appearance of this species is typically that of a sand-living form. Ferguson and Hill (1922) say: ". . . it is found on or near the sea-coast, but on several occasions it has been taken attacking the occupants of boats several miles out to sea."

This species is clearly different from the rest. Under Mr. Hardy's new classification of the Australian Tabaninae it comes in the *vetustus* group of *Dolichapha*.

CYDISTOMYIA IMMATURA, n. sp.

This species is not very closely allied to *caesius* Wlk., but is included in the same couplet for convenience, because of the lack of a distinct callus. It seems to resemble *erythrocephalus* Wulp, but differs in the more slender antennae, the much broader, shorter palpi, and the coloration of the head. It is a middle-sized, yellow and black species, all specimens of which look immature, whether they are or not.

♀. *Head.* Frons proportions 17:17:57, index $3\frac{1}{2}$, parallel. Frons brown, overlaid with yellow-brown tomentum. There may be a raised ridge (dotted line, Text-fig. 59), but this is not denuded into a shining callus in the specimens I have seen. Hairs, fine, black, rather longer at vertex. Subcallus and facial area reddish brown. Hairs, including anterior part of beard, dark brown, middle and hind areas of beard may be white. Antennae rather elongate and slender (Text-fig. 59): first two segments brown with black hairs, rest of antennae more orange. Palpi short, curved and stumpy, brown with dark brown hairs.

Thorax. Mesonotum yellow-brown, darkest towards anterior, with sutures and posterior median area of scutum paler. Hairs rather long, fine, black, intermingled with silky yellow ones; yellowish tufts on postalar calli. Pleura brown, paler anteriorly and posteriorly; hairs dark brown, paler on propleuron, pteropleuron and metapleuron.

Abdomen. Dorsum yellow-brown, with dark brown hairs. Whitish along hind margins of segments, on extreme side margins, and in a row of shallow median triangles. These areas have yellowish hairs, longer lateral pale fringes on second to fifth segments inclusive. Venter dark brown with brown hairs, segmentations yellowish with yellow hairs.

Legs. Dark yellow-brown with black hairs.

Wings. Faintly tinted with brown, especially over cross veins and along R_{2+3} and R_4 . The subcostal cell is yellow. Appendix absent or faintly indicated.

Length. Body 13 mm.; wing 13 mm.

In the British Museum is the holotype female from Cyclops Mts., Mt. Lina, 3,500 ft., iii.1936 (Cheesman). In the Archbold collection: paratype female, Rattan Camp, 3,600 ft., 17.ii.1939 (Toxopeus); one female, one male, Moss Forest Camp, 8,400 ft., 14.x.1938 (Toxopeus). In the Harvard collection, one female paratype, Morobe Dt., Surprise Creek, 26.x.19? (Stevens). In the U.S. National Museum is one female paratype from Cyclops Mts., 1,000 ft., Apr., 1945 (Jean Laffon).

CYDISTOMYIA PSEUDIMMATURA, n. sp.

Very close to *immatura*, with which I at first confused it. The most noticeable differences are in the hairs of the pleura and in the antennae, and in the female palpi.

♀. *Head.* Frons proportions 17:17:57, index $3\frac{1}{2}$, parallel, i.e. exactly the same as in *immatura*. Third antennal segment relatively shorter and broader (Text-fig. 60).

Facial area paler, contrasting with brown subcallus, and parafacials relatively broader (cf. Text-figs. 59, 60). Palpi still short, but relatively slender. Beard snow-white.

Thorax. Mesonotum (♀) with recumbent yellow hairs entirely absent. Pleural hairs almost entirely snow-white.

Abdomen. Median pale triangles almost non-existent.

Legs. Much lighter, reddish yellow, with many long pale hairs on femora.

Wings. In female holotype are paler, not marked as in *immatura*.

Length. Body 15 mm.; wing 15 mm.

♂. Eight males are available and agree in main features with the characters of the females, especially the structural differences and the colour of the pleural hairs. They show some variation in body and wing colour.

In the Archbold collection: holotype female, eight male paratypes from Iebele Camp, 6,750 ft., xi.1938 (Toxopeus); one male paratype, Moss Forest Camp, 24.x.1938 (5 Km. N. of Habbema Lake) (Toxopeus).

CYDISTOMYIA IMITANS, n. sp.

The characters given in the key distinguish this species from any in New Guinea.

♀. *Head.* Frons proportions 15:15:63, parallel, index 4. Callus short, flask-shaped, shining yellow anteriorly, becoming darker behind. Tomentum of frons golden yellow, with long dark brown hairs. A bare ocellar tubercle is present, but is not greatly swollen. Subcallus prominent and entirely bare, shining yellow. Parafacials and buccae with golden tomentum and dark brown hairs, face slightly more brown. Antennae (Text-fig. 53): first two antennal segments brown, with black hairs; rest bright orange. Palpi moderately slender, dark brown, with dark brown hairs.

Thorax. Mesonotum blackish, covered with golden yellow tomentum, which is much thicker on notopleural lobes, making these bright golden in appearance. Fine black hairs and abundant silky golden ones. Pleura in marked contrast with mesonotum, being dark brown with dark brown hairs. A little rusty-brown tomentum on sternopleuron and a few yellow hairs on prothorax.

Abdomen. Dorsum dark brown, a little paler on basal segments, venter dark brown, both with black hairs. The only yellow hairs on the abdomen are in a tiny median triangle on the first segment.

Legs. Very dark brown, almost black, knees narrowly reddish. Hairs black.

Wings. Very dark brown, slightly paler in some cells, and with a pale strip starting from vein R_4 —where it occupies half the width of cell R_4 —narrowing along wing margin almost to nothing in fifth posterior cell, then expanding again to fill the axillary area and most of anal cell.

Length. Body 12 mm.; wing 11 mm.

Holotype female, two female and three male paratypes from Araucaria Camp, 2,500 ft., 25.iii.1939 (Toxopeus), are in the Archbold collection. The holotype will be deposited in the Buitenzorg Museum, Java.

The only species known to me which resembles this is one common in collections from New Caledonia, but which appears to be undescribed. I understand that Dr. J. Bequaert is to describe this latter as new in his forthcoming paper on the Tabanidae of the Pacific Islands. In order not to prejudice his description I will say no more than that the two species are abundantly distinct, perhaps not even closely related, yet show remarkable agreement in the general pattern of coloration. This suggests that they may both mimic some other insect, probably a Hymenopteron, the mimetic resemblance having developed independently in the two areas. There are some bees of the genus *Megachile* that have this general appearance, but I have not been able to find an exact model.

CYDISTOMYIA FESTIVA, n. sp.

A strongly-marked, orange and black species, the abdomen bright orange on four basal segments, rest black. Wings darkened, appendix present. In general appearance

this closely resembles *chrymater* S.S., from Java, but differs from that species in having the subcallus and facial area yellow instead of chocolate-brown; beard yellow instead of black; thorax without pale longitudinal stripes; wings with long appendix.

♀. *Head*. Frons proportions 8:12:44, index 4, strongly diverging towards antennae. Callus prominent, a tapering ridge (Text-fig. 55). Well-marked ocellar tubercle present. Tomentum of frons yellow, with black hair. Subcallus and entire facial region with thick yellow tomentum; hairs mainly black on parafacials, hairs of face mixed black and yellow, beard yellow. Antennae (Text-fig. 55): first segment rather long, third segment almost equal to the terminal segments; first two segments light brown, with black hairs externally and orange hairs dorsally and ventrally; rest bright orange, only the extreme tip slightly browned. Palpi very slender, orange; hairs rather long and drooping, mainly orange basally, mainly black towards apex of palpi. In dried specimens the eyes may still retain a vivid green colour and show one broad purple band from the antennal angle of the eye.

Thorax. Mesonotum uniformly covered with thick greenish yellow tomentum, with a few fine black hairs, but silky yellow hairs are especially numerous posteriorly, and all side tufts almost entirely yellow. Pleura mainly with yellow tomentum and yellow hairs, but with brown tomentum and dark brown hairs on ptero- and hypopleura and on coxae. The metapleura and its tuft, however, are yellow.

Abdomen. First four segments bright orange, with orange hairs, the first tergite with some black hairs. Fifth to seventh sternites black, with black hairs, but anal lamellae appear to be orange. Venter similar.

Legs. Coxae and femora dark brown, tibiae somewhat lighter, tarsi dark, all with black hairs.

Length. Body 10 mm.; wing 10 mm. (One specimen is much smaller than the others, about 8 mm. long.)

In the British Museum are the holotype and four female paratypes from Japen Is., Camp 2, Mt. Eiori, 2,000 ft., x.1938 (Cheesman).

CYDISTOMYIA DIMORPHA, n. sp.

A small species (8 mm.) showing marked sexual dimorphism. The female is black, with transverse white bands on both thorax and abdomen; the male has a similar thorax, but the first two abdominal segments are pale yellow, contrasting with the following segments. In this the males resemble *basalis* Mcq., but are distinguished at once by the grey transverse bands on the thorax.

♀. *Head*. Frons proportions 8:10:35, index 3½. Callus as in Text-fig. 56, without very great anterior expansion. Tomentum grey, black about region of ocellar callus, which is very faintly indicated. Subcallus with dark brown tomentum, contrasting sharply with grey of parafacials, buccae and face; there is brown tomentum about bases of proboscis and palpi, extending across to each eye margin. Hairs white, except on brown area, where they are dark brown. Beard unusually sparse. Antennae (Text-fig. 56): first antennal segment rather long, third of unusual shape, resembling that of *Haematopota*. Rather blackish brown, with black hairs, and some pale hairs ventrally on first two segments. Palpi elongate, blackish, with white hairs at base, otherwise with mainly black hairs.

Thorax. Mesonotum and pleura dark nigger-brown, with two white or greyish transverse bands which cross the mesonotum and extend down the pleura on each side. One band lies on the transverse suture and includes the notopleural lobes, and the anterior pleura up to the middle of the mesonotum; the other comes immediately before the scutellum, passing behind the wing base and including the metapleuron. Scutellum dark nigger-brown.

Abdomen. Dorsally and ventrally dark nigger-brown, with dark brown hairs, hind margin of each segment with a clear-cut narrow white band, not at all raised into median triangles, and with white hairs. Seventh tergite mainly white.

Legs. Dark brown, with dark brown hairs.

Wings. Faintly tinted brownish, more strongly so along costal margin and at tips of radial veins. Vein R_4 without appendix.

Length. Body 8 mm.; wing 8 mm.

♂. Differs from female in following particulars: no brown patch on each parafacial; whole of second abdominal segment and parts of first and third are translucent yellow, both dorsally and ventrally.

Holotype female and two male paratypes from Araucaria Camp, 2,500 ft., iii.1939 (Toxopeus) are in the Archbold collection.

In the British Museum is one male paratype from Japen Is., Mt. Eiori, 2,000 ft., xi.1938 (Cheesman).

The position of this species is somewhat anomalous. In venation as well as in general appearance it may be allied to *Chasmia basifasciata* de Meij., but the antennal structure is different.

CYDISTOMYIA LAETUS.

Tabanus laetus de Meijere, 1906, *Nova Guinea*, v, p. 74; Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 391; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 334.

A smallish (10 mm.) dark brown species, with white scutellum, prominent median and lateral abdominal triangles, and a strong brown stain along costal margin of wing.

♀. *Head.* Frons proportions 10:10:47, index 5, parallel. Callus with small anterior portion, and spindle-shaped median extension (Text-fig. 24). Tomentum of frons grey, brown near callus. Subcallus golden brown; face light brown in middle, white at sides; parafacials and buccae white, with white hairs and beard. Antennae (Text-fig. 24): reddish, basal segments with black hairs, fourth to seventh segments slightly darker. Palpi bulbous basally, tapering to a long, fine point, dark brown with black hairs.

Thorax. Mesonotum chestnut-brown, with black hairs, fading to white with white hairs on all borders, including anterior border of scutum, and whole of scutellum; notopleural area is left dark brown. Pleura mainly white, with white hairs, sternopleuron brownish. Fore coxae rather brownish, with some pale brown hairs, other coxae white with white hairs.

Abdomen. Dorsum dark brown with brown hairs, each segment with a large and clearly-defined white median triangle with white hairs, and a similar pair of lateral triangles. Venter dark brown, with white segmentations.

Legs. Femora chestnut brown, tibiae more yellowish, tip of fore tibiae and all tarsi black-brown, hairs black.

Wings. Slightly stained yellow, and deeply browned along fore border up to vein R_1 , and round costa as far as vein M_2 . No appendix.

Length. Body 10 mm.; wing 10 mm.

The holotype (female) of this species, from "New Guinea", is in *Natura Artis Magistra*, Leyden, with females from Etna Bay, the Lorentz area and Vertseeg's area. In the British Museum are two paratypes from Heuvelbivak (Lorentz), and two females from Papua, Mafulu, 4,000 ft., xii.1933 (Cheesman). In the School of Public Health and Tropical Medicine, Sydney, are two females from Papua, Mondo, 4,750 ft. (Stewart), and two females, Finsch Haven (Wagner). Stekhoven also records it from the Bougainville Mts.

CYDISTOMYIA ALUENSIS, n. sp.

A middle-sized black species, slender in build, with white scutellum and white abdominal segmentations, very slightly raised into median triangles. Wings darker along fore border, antennae and legs black. Differs from *albidosgmentatus* S.S. in having black palpi and legs, and brown-stained wings.

♀. *Head.* Frons proportions 15:13:60, index 4, very slightly tapering. Callus as in Text-fig. 65, tomentum greyish, with black hairs. Subcallus with dark brown tomentum, contrasting strongly with white parafacials. Centre of face slightly brownish, otherwise entire facial area white with white hairs; beard white. Anterior tentorial pits are

unusually deep, and almost circular. Antennae (Text-fig. 65); black with black hairs, only extreme base of third segment reddish. Palpi black, with black hairs.

Thorax. Tomentum of mesonotum; anterior half, back to transverse suture and a little beyond it in middle, ashy grey, with three narrow brown longitudinal stripes; posterior half of scutum dark reddish brown; lateral margins and scutellum white or whitish; notopleural lobes brown. Dark areas with black hairs, pale areas with white ones. Pleura greyish, more brownish on parts of mesopleuron and sternopleuron, hairs snow-white.

Abdomen. Dark brown. Extreme lateral margins of first tergite and hind margins of second, third and fourth segments are white, the white segmentations being slightly expanded laterally and medially. Venter similar, without marked expansions of segmentations, fifth and sixth segments all dark brown.

Legs. Coxae with many brown hairs. Legs black or very dark brown, knees pale, hairs black.

Wings. Stained yellow-brown, more deeply so on foreborder and radial veins. Small trace of appendix.

Length. Body 12 mm.; wing 11 mm.

Holotype female, 15 female paratypes, from mountain slope above Bernhard Camp, 2,100 ft., 16.iii-10.iv.1939 (Toxopeus); other paratypes; one female, Bernhard Camp, hills near Alu Camp, 1,800-2,400 ft., 5.xi.1938 (Olthof); two females Araucaria Camp, 2,400 ft., 21-23.iii.1939 (Toxopeus): one female Rattan Camp, 3,600 ft., 24.iii.1939 (Toxopeus). All the above in the Archbold Collection, type to be deposited in the Buitenzorg Museum Java.

Miss Cheesman collected three females on Waigeu, Camp Nok, 2,500 ft., iv.1938, and W. Stüber one female at 140°E, 3°10'S, Jan., 1937-8, 900-1800 ft. These specimens may represent a variety of this species. They are rather smaller and slighter in build, flagellum of antennae narrower, beard brown instead of white. They are not in good condition.

CYDISTOMYIA NIGERRIMA, n. sp.

Very similar to *immigrans*, but blacker in appearance, femora all dark, costal cell yellowed. It is possible that this is only a dark form of *immigrans*, but the two occur in the same area.

♀. *Head.* Frons proportions 11:13:56, index $4\frac{1}{2}$, slightly divergent. Tomentum of frons grey at sides, brown in middle. Callus with prominent lower part and stout median extension (Text-fig. 70). Subcallus with thick dark brown tomentum. Rest of facial area contrasting, white, with white hairs, including beard. Antennae (Text-fig. 70): first two segments brown, with black hairs; third segment orange; terminal segments blackish, together fully as long as third segment. Palpi black with black hairs, except for white hairs on basal segment.

Thorax. Mesonotum as in *immigrans*, chestnut brown, with grey tomentum at sides and on sutures, greenish grey when seen from behind, with fine black hairs and silky greenish ones. Notopleural lobe more strikingly dark, so that a very distinct blackish band runs along notopleural suture. Pleura grey, with white hairs.

Abdomen. Dark brown with white segmentations and black hairs, a little reddish towards base. White hairs along segmentations, with indications of shallow median and lateral triangles. Venter similar, some greyish tomentum on first two segments, extending up into a tomentose spot on each side of first tergite.

Legs. All femora shining dark brown or black. Fore tibiae yellow on basal two-thirds, apical third and tarsi black; middle and hind tibiae, and first tarsal segments yellow, rest of tarsi black. Hairs black.

Wings. Almost hyaline, except that costal cell and anterior half of first basal cell are clear yellow, and costal margin is slightly browned between stigma and apex of wing. R₁ with only a trace of an appendix.

Length. Body 9 mm.; wing 11 mm.

Holotype female from Milne Bay, Feb., 1943 (Mackerras) is in the collection sent to me by Mr. D. J. Lee. In the U.S. National Museum are two paratypes, one female Maffin Bay, 20 Oct., 1944; one female Nadzab, Markham R. Valley, July, 1944 (Krombein). In the School of Public Health and Tropical Medicine, Sydney, is a specimen from Fly R. (Strong) which appears to belong to this species, though the abdomen (denuded) is more reddish and more elongate.

CYDISTOMYIA IMMIGRANS, n. sp.

Closely allied to *T. sequens* Wlk., from Queensland, but I think it is distinct. The mesonotum lacks the underlying grey colour of *sequens* and other allied species, the frons is narrower, and the antennae rather different.

♀. *Head.* Frons proportions 11:11:48, index $4\frac{1}{2}$, parallel. Tomentum of frons yellow, with dark brown hairs. Subcallus golden brown, contrasting with entire facial area, which is white with white hairs. Antennae (Text-fig. 64): first two segments brown with black hairs; third segment redder, following segments black. Palpi yellow or blackish, first segment with white hairs, second with mainly black hairs.

Thorax. Mesonotum light chestnut, with paler tomentum on sutures and margins; a greenish appearance when seen from behind. Scutellum more reddish in ground-colour. In well-preserved specimens there are a pair of triangular, whitish tomentose spots immediately before scutellum. Fine clothing hairs are black, intermingled with some silky greenish ones, and with paler hairs more numerous at sides and posteriorly. Pleura white, with white hairs, rather long and thick on pro- and metapleura.

Abdomen. Dorsum yellow-brown basally, darker apically, with segmentations narrowly white. Median pale triangles merge into an indistinct stripe; extreme lateral margins of segments are white, forming a white stripe along each side of dorsum. Hairs brown on most of brown area, and overlapping a little into brown areas. Venter greyish, with mostly white hairs.

Legs. Mainly reddish yellow, tips of tibiae and tarsi blackish. Some grey dusting on femora, especially on basal third of hind femora. On some specimens the entire foreleg may be more blackish. Some whitish hairs on femora, and yellowish ones on tibiae, otherwise hairs mainly black.

Wings. Clear hyaline, except for a narrow browning along costa, most marked at tips of radial veins. Stigma pale yellow. No appendix. Costal cell hyaline.

Length. Body 10 mm.; wing 9 mm.

In the British Museum are the holotype female and two female paratypes from Papua, Kokoda, 1,200 ft., ix-x.1933 (Cheesman); one female Huon Gulf, Morobe Dt., 22.v-19.vi.1937 (Froggatt). In the School of Public Health and Tropical Medicine, Sydney, six females, N.E. Papua, Mt. Lamington, 1,300-1,500 ft. (McNamara); one female Madang (Lohe); one female Buldo, 2,200 ft. (Taylor); one female Buna Bay (McNamara); one female Papua, Goodenough Is. (Clinton); two females Lae, 1947 (Bayley). In the U.S. National Museum are two females from Cyclops Mts., 1,000 ft., Feb. and Apr., 1945 (Jean Laffon), which seem to belong to this species, though the legs are somewhat darker.

CYDISTOMYIA INOPINATA, n. sp.

Nearly related to *immigrans*, from which it differs in being slightly longer and more robust, in having a different callus, and in the terminal antennal segments not being darkened.

♀. *Head.* Frons proportions 12:12:56, index $4\frac{1}{2}$, parallel. Tomentum of frons greyish yellow, with yellow hairs. Callus (Text-fig. 69) pale yellow. Subcallus with golden brown tomentum, contrasting with the white tomentum and white hairs of facial area. Beard white. Antennae (Text-fig. 69): first two segments yellow-brown, with black hairs; third segment bright orange; other segments slightly darker, but not black. Palpi whitish, hairs white on first segment, otherwise mainly black.

Thorax. Mesonotum reddish yellow, overlaid with greyish tomentum, especially thick anteriorly and just before scutellum, clothed with fine black hairs and recumbent silky yellow ones. Pleura with thick whitish tomentum and white hairs.

Abdomen. Dorsum yellow-brown, obscurely darker apically, hind margins of segments whitish. Hairs mainly black; whitish hairs in large median triangles and on hind margins, especially towards sides. Venter similar, but without median triangles, and with more numerous whitish hairs on disc.

Legs. Yellow-brown, femora with a little grey dusting, tarsi darker. Hairs largely black on dorsal face, and on tarsi, some whitish hairs ventrally.

Wings. Hyaline, only stigma clear yellow, or slightly tinted along veins. R_4 with very short appendix, or a mere trace.

Length. Body 13 mm.; wing 12 mm.

Female holotype and one female paratype, Morobe Dt., Surprise Creek (Stevens), are in the Harvard Museum of Comparative Zoology.

CYDISTOMYIA HEYDONI, n. sp.

Superficially very like *T. semicircularis* Ric. and *T. exagens* Wlk. The general pattern is so similar that at first sight it would seem that any system that separates this species from the *semicircularis* group must be an artificial one. Yet it has a bare subepaulet, thoracic spiracles without lips, and a broader, more parallel-sided frons. I think there is no doubt that *heydoni* belongs to *Cydistomyia* as I am using the term, and that the resemblance to *semicircularis* is convergent. This is confirmed by other minor details such as the entirely different pattern and hair-covering of the mesonotum.

I have pleasure in naming this species after Dr. G. A. M. Heydon, who collected some of the type material, and who very kindly communicated my earlier paper to the Linnean Society of New South Wales.

♀. *Head.* Frons proportions 19:19:52, index $2\frac{3}{4}$, parallel. Callus very short, with short linear extension, the whole centre of frons distinctly bulbous (Text-fig. 68). Tomentum of frons white immediately above callus, and narrowly along eye margins, almost to vertex, but dark brown with black hairs on most of upper two-thirds of frons. Subcallus dark brown tomented, strongly contrasting with entire facial area, which is white with snow-white hairs. Antennae (Text-fig. 68): black with black hairs. Palpi somewhat variable in shape and colour, whitish internally, with greyish or grey tomentum externally, and white or black hairs.

Thorax. Mesonotum boldly marked in dark brown and grey. Brown markings are: a broad median stripe, tapering sharply in its hinder half to about one-quarter of its former width, then reaching scutellum, where it expands again to occupy half width of scutellum. On each side of this median stripe is a broad lateral stripe, narrowly interrupted at transverse suture, which leaves bare the entire lateral border, including notopleural lobes. Between these stripes tomentum is grey. Two kinds of clothing hairs, longer and silky, shorter and stiff. Both these are black on the brown areas, white on pale areas. Pleura with greyish tomentum and entirely silvery hairs.

Abdomen. Dorsum mainly dark brown, with a pattern similar to that of *exagens* Wlk.: i.e., first segment is indistinctly whitish in middle; second segment has a pair of crescentic transverse marks anteriorly and a shallow median triangle behind; four following segments have pale median triangles of diminishing size; each segment with lateral triangles, which unite into a pale band along side margins. Venter mainly dark brown with very narrow pale segmentations expanding into small lateral triangles. Hairs black on dark areas, white on pale areas.

Legs. Forelegs black with black hairs, except for tibiae, which are reddish, with pale hairs on basal half. Middle and hind legs reddish, femora a little darkened dorsally, tarsi and tips of tibiae blackish. Hairs dark on dark areas, white or whitish elsewhere, especially on femora.

Wings. Quite clear, without any brown colouring. R_4 with a very short appendix, or with merely an indication of one.

Length. Body 11–13 mm.; wing 11 mm.

♂. Closely similar, and can be named from key.

In the British Museum is the holotype female, Upper Ramu R. (Bearup). Paratypes: in the School of Public Health and Tropical Medicine, Sydney, four females, Ai-ura,

Upper Ramu R. (Heydon); one female Upper Ramu R. (Heydon). In the Archbold Collection one female, Baliem Camp, 5,000 ft., 9.xii.1938 (Toxopeus); one female Iebele Camp, 7,000 ft., 5.xi.1938 (Toxopeus); one female Moss Forest Camp, 28.x.1938 (9 km. N. from Habbema Lake) (Toxopeus).

CYDISTOMYIA MISIMENSIS, n. sp.

This species is represented by three very poorly preserved females in the Harvard Museum of Comparative Zoology. Because of the state of the specimens it is scarcely possible to give any detailed description, but as the species is clearly related to *heydoni*, yet abundantly distinct, it is possible to give a few diagnostic characters. It differs from *heydoni* in the following details.

♀. *Head*. Frons slightly narrower, proportions about 13:13:46, index $3\frac{1}{2}$. Antennae black, but third segment relatively more slender, and following segments relatively shorter (cf. Text-figs. 66, 68).

Thorax. Mesonotum much denuded, but seems to lack the distinctive pattern of *heydoni*, and may be almost uniformly greyish.

Abdomen. Pattern of dorsum similar, but the hind margins of the segments are pale, whereas in *heydoni* the triangles are quite isolated.

Legs and wings generally agree with the description given for *heydoni*.

Length. Body 9–10 mm.; wing 9 mm.; much less robust than *heydoni*. In the Harvard Museum of Comparative Zoology, three co-type females, Morobe Dt., Mt. Misim (Stevens).

CYDISTOMYIA BISECTA, n. sp.

Represented by a unique specimen, this species is set apart from any other in New Guinea, except *T. latisegmentatus* S.S., by the peculiar patterning of the thorax. From *latisegmentatus* it differs in numerous details of colour.

♀. *Head*. Frons proportions 13:13:65, index 5, parallel. Callus mahogany-brown, an elongate spear-shape, almost completely filling frons at its lower end (Text-fig. 63). Tomentum of frons very narrowly yellow along lower eye margin, elsewhere dark brown with black hairs. An indistinct ocellar triangle and three vestigial ocelli can be seen. Subcallus with golden brown tomentum, face centrally dark brown, rest of face, parafacials and buccae bright lemon-yellow. Hairs dark brown on face and parafacials, elsewhere yellow. Antennae (Text-fig. 63): bright orange, two basal segments with black hairs. Palpi blackish brown with black hairs.

Thorax. Mesonotum dark brown with black hairs, overlaid anteriorly—i.e. before transverse suture—with greyish yellow tomentum and pale hairs. Humeri and notopleural lobes yellow, with long yellow hairs; supra-alar and postalar calli brown, with black hairs. Pleura divided horizontally into an upper bright yellow area with yellow hairs and a lower dark brown area with black hairs. Dividing line is the horizontal suture dividing mesopleuron from sternopleuron.

Abdomen.—Dark brown with black hairs, without any paler hairs or pattern, except at sides of extreme base, where there is a lemon-yellow patch with yellow hairs.

Legs. Dark brown, with black hairs.

Wings. Slightly tinted yellow all over, much more darkly stained in costal and basal cells. Darkening in basal cells extends over cross-veins and joins up with stigma, giving a suggestion of a cross-band.

Length. Body 11 mm.; wing 10 mm.

The unique female holotype, from Bernhard Camp, 1,800–2,000 ft., 5.xi.1938 (Olthof), is in the Buitenzorg Museum, Java.

CYDISTOMYIA NOKENSIS, n. sp.

Allied to *solomonensis* Ric., but distinguished from that species by the slightly broader frons, which is narrowest at antennae, and by the callus, which is more expanded at its lower end (cf. Text-figs. 22, 62). Closely resembles description of *olivaceus* S.S., but differs in longer third antennal segment and in entirely clear apex of wing.

♀. *Head*. Frons proportions 12:8:63, index 8, tapering. Callus shaped as in Text-fig. 62, pale yellow. Subcallus and entire facial area pale yellow, with yellow hairs, except for dark brown hairs on parafacials and buccae. Antennae (Text-fig. 62): pale reddish yellow, basal segments with a few orange hairs, but mostly with black hairs. Palpi yellow, with mostly yellow hairs. Proboscis yellow, labella about half total length.

Thorax. Mesonotum yellow-brown with black hairs, a few yellow hairs on lateral calli. Pleura yellow with yellow hairs.

Abdomen. Dorsally and ventrally yellow-brown on first two segments, or thereabouts, becoming black-brown apically; hairs black. No pale triangles.

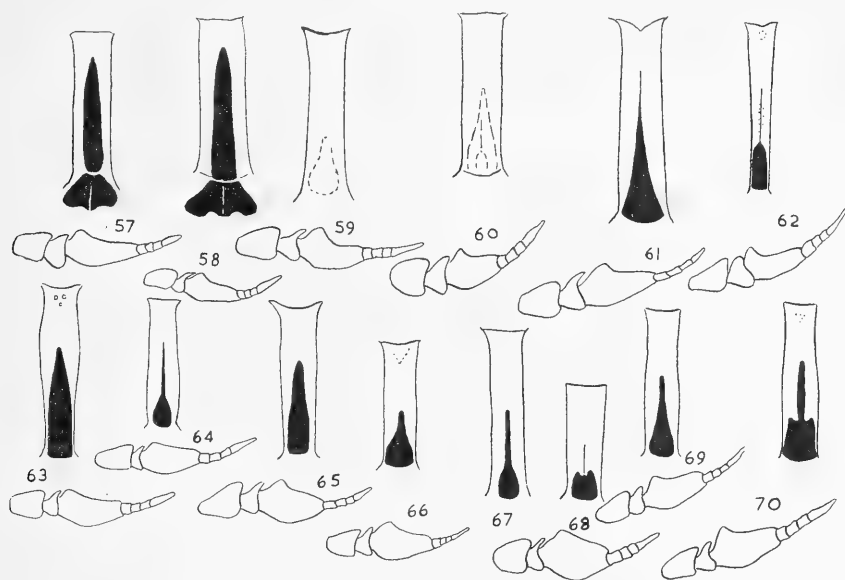
Legs. Femora reddish yellow, with mainly red hairs; tibiae and tarsi darker, with black hairs.

Wings. Clear, only yellowed in costal and first basal cells. R_4 without appendix.

Length. Body 12 mm.; wing 11 mm.

♂. Similar, hairs of mesonotum longer. This is one of the species of which the males can really only be named by association with the females.

Female holotype, one female, one male paratypes, Waigeu, Camp Nok, 2,500 ft., iv.1938 (Cheesman), in the British Museum. In the U.S. National Museum, one female paratype from Hollandia, May, 1945 (Malkin).



Text-figures 57-70.

Figs. 57-70. Frons and antennae of female: 57, *Chalybosoma luciliaeformis*, n. sp.; 58, *Chal. malkini*, n. sp.; 59, *Cyd. immatura*, n. sp.; 60, *Cyd. pseudimmatura*, n. sp.; 61, *Cyd. oudella*, n. sp.; 62, *Cyd. nokensis*, n. sp.; 63, *Cyd. bisecta*, n. sp.; 64, *Cyd. immigrans*, n. sp.; 65, *Cyd. aluensis*, n. sp.; 66, *Cyd. misimensis*, n. sp.; 67, *Cyd. crepuscularis*, n. sp.; 68, *Cyd. heydoni*, n. sp.; 69, *Cyd. inopinata*, n. sp.; 70, *Cyd. nigerrima*, n. sp.

CYDISTOMYIA OUDELLA, n. sp.

Although the unique female of this species was somewhat damaged during its original pinning, the characters given in the key enable it to be recognized as distinct.

♀. *Head*. Frons proportions 9:13:50, index 4, frons diverging towards antennae, with slightly concave sides (Text-fig. 61). Callus an elongate pyramid with concave sides. Tomentum of frons brownish yellow, with black hairs. Subcallus, parafacials

and buccae with golden-brown tomentum and brown hairs, which become black in beard. Face largely brown, shining yellow-brown. Antennae (Text-fig. 61): first two segments yellow-brown with black hairs; third segment dark red-brown basally, yellow apically above, following segments dark red-brown. Palpi yellow-brown, with black hairs, rather long.

Thorax. Mesonotum light brown, with abundant silky yellow-brown hairs; the fine erect hairs are mainly black or brown, but with many yellow ones, especially on the sides and hind margin. Pleura yellow-brown with yellow hairs.

Abdomen. Dorsally and ventrally reddish brown with orange hairs, disc of each segment rather darker, hind margin rather lighter.

Legs. Yellowish with orange and yellow hairs on femora and bases of tibiae, black hairs on tarsi and tip of fore tibiae giving these areas a darker appearance.

Wings. Yellowed as far back as vein Cu_1 , colour becoming deeper towards fore border. Base of R_4 quite rectangular and with moderately long appendix.

Length. Body 11 mm.; wing 12 mm.

In the British Museum is the holotype female, a unique specimen from Japen Is., Camp 3, Central Range, Mt. Oud, 3,500 ft. (Cheesman).

CYDISTOMYIA SOL.

Tabanus sol Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 450.

A species recognized by the predominantly pale yellow colour of the tomentum and hairs in almost every part. The holotype was originally named *insurgens* by Miss Ricardo, and I think Stekhoven was right in removing it from that species because of the broader third antennal segment. I am not certain that the specimens listed below all belong to one species, since there is variation in antennal shape, wing colour and venation, but I am not prepared to split the material further. The description below is taken from Stekhoven's type in the British Museum.

♀. *Head.* Frons proportions 11:10:50, index 5, nearly parallel. Callus (Text-fig. 21) pale yellow, somewhat abraded. Tomentum of frons, subcallus and entire facial area bright yellow; some black hairs towards vertex, hairs otherwise entirely yellow. Antennae (Text-fig. 21): entirely yellow, with yellow hairs, only those on terminal segments brownish. Palpi yellow, with yellow hairs.

Thorax. Mesonotum and pleura entirely yellow, with yellow hairs.

Abdomen. Dorsally and ventrally yellow with yellow hairs, a little more reddish, or even blackish, towards apex, with a few black hairs on terminal segments.

Legs. Bright yellow or orange, with yellow hairs, a few black hairs on tarsi.

Wings. Veins yellow. Membrane faintly tinted brownish overall, a clearer yellow in costal cell, but not brown on fore border. R_4 (in holotype) almost rectangular, but without appendix.

Length. Body 11 mm.; wing 10 mm.

In the British Museum are the holotype female from Bivak Is., 25.ii.1910, and two females from Rivierkamp, ii.1910 (all Lorentz); two males, two females, 140° E., 3° 10' S., 900-1,800 ft., Jan., 1937-8, and one male, three females, Humboldt Bay Dt., Bewani Mts., ix.1937 (W. Stüber); two males, one female, Waigeu, Camp Nok, 2,500 ft., iv.1938 (Cheesman).

In the School of Public Health and Tropical Medicine, Sydney, one male, one female, Waroo, Finsch Haven (Wagner), and one male, Aru Is., Vesi Is. (Littlechild); one female, Mamberamo, Albatros Bivak, 1926 (v. Leeuwen).

One or two specimens have a shorter radial fork, with more pronounced appendix, with or without dark hairs on the palpi. Stekhoven (1926, p. 451) mentions similar variations in some of the specimens he saw, which he did not consider could be recognized as new species.

CYDISTOMYIA LORENTZI.

Tabanus lorentzi Ricardo, 1913, *Nova Guinea*, ix, zool. 3, p. 400; Schuurmans Stekhoven, 1926, *Treubia* vi, suppl., p. 447.

This species is bigger, redder on the abdomen, and generally less uniformly yellow than *sol*, but is difficult to define by any absolute characters. Generally the palpi and legs have many more dark brown or black hairs, and the beard in typical specimens is brown. The frons is somewhat broader, if anything slightly diverging towards the antennae, and the callus extends only half-way towards the vertex (in most specimens of *sol* it extends three-quarters of the way or more). Labella of proboscis shorter than in *sol*.

♀. *Head*. Frons proportions 14:16:67, index $4\frac{1}{2}$, almost parallel, but slightly narrower in middle. Callus shining reddish brown (Text-fig. 19). Tomentum of frons greyish yellow, with mainly yellow hairs. Subcallus yellow-brown, with the hairs, including beard, yellow-brown or brown. Antennae (Text-fig. 19): first two segments brown with black hairs, third orange, later segments blackish brown. Palpi pale brown, with dark brown hairs. Proboscis yellow-brown basally, black at tip, labella about two-fifths length of proboscis.

Thorax. As in *sol*, entirely yellow, with yellow hairs (paratype) or, more often, reddish yellow, with orange hairs.

Abdomen. Dorsally and ventrally reddish brown, with orange hairs, which are more brownish or blackish on disc and more yellowish on segmentations.

Legs. Reddish, with mainly black pubescence.

Wings. In paratype, clear, only pale yellow in costal and first basal cells. In most other specimens before me the membrane is more or less stained yellow. Vein R_4 without appendix.

Length. Body 13 mm.; wing 13 mm.

Holotype female from Alkmaar, Oct., 1909 (Lorentz), is in *Natura Artis Magistra*, Leyden. In the British Museum is a paratype from the same locality.

The rest of the material shows a good deal of variation. Specimens are generally darker than the paratype and the wings more deeply stained yellow; the beard is often yellow. It may at some time be necessary to subdivide this material.

In the British Museum: two females, Papua, Mafulu, 4,000 ft., i.1934 (Cheesman). In the Archbold collection: nine females, Bernhard Camp, 150 ft., viii.1938 (Olthof); two females, Bernhard Camp, 1,800-2,500 ft., 5.xi.1938 (Olthof); one female, Bernhard Camp, 150 ft., 23.xii.1939 (? 1938) (Toxopeus); three females, Hollandia, vii.38 (Toxopeus); one female, Bernhard Camp B, 300 ft., 7.iv.1939 (Toxopeus).

In the School of Public Health and Tropical Medicine, Sydney: one female, Papua, Port Moresby, Jan., 1941 (Taylor); one female, Papua, Waria R., 21.ii.36 (Littlechild). The latter specimen is much darker even than the rest, and has many black hairs dorsally on the abdomen.

Two females in the British Museum from Wakwa Exp., Dec., 1912, Camp III, 7,500 ft. (Boden Kloss), may represent a new species, but are too shrivelled and denuded to be sure of this. The blackish palpi are more elongate than in *lorentzi* and the frons (partly shrivelled) appears slightly divergent. Terminal antennal segments black.

CYDISTOMYIA CREPUSULARIS, n. sp.

The unique female specimen is greasy, but the bushy, dark brown hair-covering sets it apart from any other *Cydistomyia*. In appearance it resembles the *obscuratus*-group of *Tabanus*, but it is distinguished at once by the bare subepaulets and the broader, parallel-sided frons.

♀. *Head*. Frons proportions 12:13:62, index 5, nearly parallel. Callus small, contracting smoothly into a long median extension (Text-fig. 67). Tomentum of frons dark brown, with black hairs. Subcallus and entire facial area brown, with dark brown hairs, beard dark brown. Antennae (Text-fig. 67): first two segments dark brown with black hairs, rest missing. Palpi dark brown with black hairs.

Thorax. Mesonotum (greasy) very dark red-black, humeri reddish. Black hairs rather long and dense; silky yellow hairs are present, but inconspicuous. Pleura black-brown, with bushy dark brown hairs.

Abdomen (greasy). Dorsum dark red basally, black apically, venter black, both with entirely dark brown hairs; no pale hairs, even on side margins.

Legs. Femora a very dark mahogany-red, black above; tibiae and tarsi black or very slightly brownish. Hairs black.

Wings. Faintly tinted yellowish along veins, costal cell and stigma clear yellow. R_4 without appendix.

Length. Body 12 mm.; wing 12 mm.

The unique holotype female, from Haumo R., val., Milne Bay, 25.iii.1944 (Krombein), is in the U.S. National Museum.

This specimen is annotated: "collected at light", and its sombre appearance is consistent with a crepuscular habit. Possibly it is no more than a melanistic form of *lorentzi* Ric.

OTHER SPECIES RECORDED FROM NEW GUINEA.

I have not recognized the following species, which are recorded from New Guinea:

1. *T. latisegmentatus* S.S., 1926, p. 294. My *bisecta*, n. sp., may be a form of this, but differs in a number of details of colouring. Holotype, from the Lorentz area, is in Natura Artis Magistra, Amsterdam.
2. *T. bipunctatus* S.S., 1926, p. 519. Seems to be close to *nigerrima*, n. sp., but differs in having a narrower frons and callus and in having golden hairs instead of white ones in the abdominal triangles. Holotype, from Idenburg River, is in Natura Artis Magistra, Amsterdam.
3. *T. griseiventer* S.S., 1926, p. 288. A grey species, frons almost parallel, index 4-6. Thorax and base of abdomen grey, rest of abdomen more brownish, but with grey tomentum. Legs brownish. Wings clear, with short appendix. Holotype, from Noord River (i.e. Lorentz R.), in Natura Artis Magistra, Amsterdam.
4. *T. olivaceus* S.S., 1926, p. 453. Closely resembles *Cydistomyia nokensis*, n. sp., but appears to be distinguished by the broader third antennal segment and the shorter terminal segments. The wing tip is browned. Holotype, from south New Guinea, is in Natura Artis Magistra, Amsterdam.
5. *T. albidosegmentatus* S.S., p. 332. Seems to be quite close to *C. aluensis*, n. sp., but differs in having pale, white-haired palpi and pale yellow femora and tibiae. Holotype, from the Lorentz area, is in Natura Artis Magistra, Amsterdam.
6. *T. aroensis* S.S., 1926, p. 448. Close to *oudella*, n. sp., but differs in having darker legs, the black-haired abdominal tergites, and in shape of frons, which is nearly parallel, or converging slightly towards antennae. Holotype, from Dobo, Aroe Is., in Vet. State lab., Buitenzorg, Java.
7. *T. selene* S.S., 1926, p. 292. A blackish species with half-moon-shaped, white abdominal spots. May be close to *aluensis*, n. sp., but has a narrower frons and differently marked wings. Holotype, from the Lorentz area, is in Natura Artis Magistra, Amsterdam.
8. *T. erythrocephalus* Wulp, 1868, *Tijdsch. v. Ent.*, xi, p. 99; Schuurmans Stekhoven, 1926, p. 419. A brown-black form, without a shining frontal callus. It resembles *immatura* and *pseudimmatura*, n. spp., but differs, as mentioned, in the descriptions of those species. Holotype, from Halmahera, is in the Rijksmuseum of Natural History, Leyden.
9. *T. monoculus* Dol., 1858, *Natuurk. Tijd. Ned. Ind.*, 17, p. 85. Wulp, in his Catalogue of the Diptera of South Asia, mistakenly gave the locality of this species as Amboina and was copied by later authors. The correct locality is "Midden-Java (Gombong)", and the species should therefore be struck off the New Guinea list.
10. *T. yulensis* v. Roder, 1892, *Stett. ent. Zeit.*, 53, p. 244. This species has apparently never again been recognized, so I repeat the original description. "Epistoma

yellow-haired. Callus linear, red-black, shining; eyes bare; antennae pitch-black, third segment with distinct tooth; palpi pitch-black, with very short black hairs. Thorax dorsally, including scutellum, pitch-black; breast greyish yellow pollinose and yellow-haired; abdomen brown, with golden hairs laterally: venter brown, hind margins of segments golden. Wings weakly brownish. Halteres yellow. Legs black, hind tibiae with black fringe. Length 21 mm. Habitat: Mt. Yule, N. Guinea."

Note that the locality is not Yule Island, but Mt. Yule, 9,500 ft., on the mainland, 08° 15' S., 146° 40' E.

From its size, linear callus, and generally black appearance, this would seem to be a *Tabanus* near *wollastoni* or *pollinosus* Ric., but neither species has golden hairs on the abdomen as he describes.

11. *T. argentsignatus* S.S., 1926, p. 364. Timor.

12. *T. obtusipalpis* S.S., 1926, p. 498. Mysol Is.

The types of these two species are said to be in the British Museum, but I have not been able to trace them.

ADDENDA TO PRECEDING PART OF THIS PAPER.

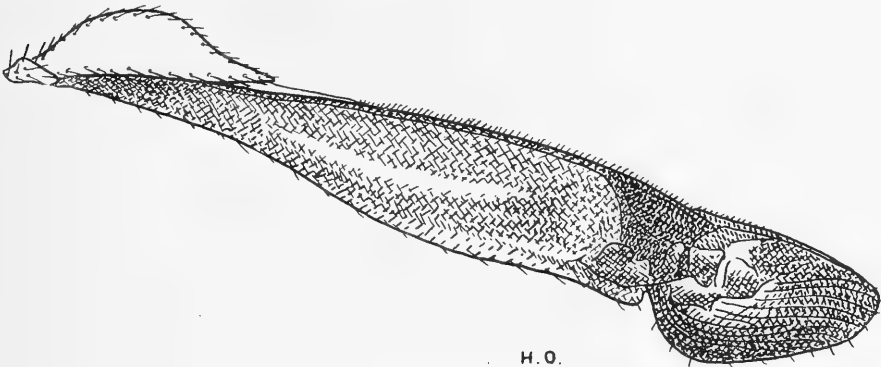
After the preceding part of this paper (these PROCEEDINGS, lxxii, 1947, 125-142) had been sent to press, the following additional information came to light.

SCAPTIA BERNHARDI Oldr.

One female in a collection received from the S. Australian Museum. N. New Guinea, Mt. Lucreu, 2,000 ft., Jan., 1939 (Miss Cheesman).

SCAPTIA MAFULENSIS Oldr.

In a collection from the Harvard Museum of Comparative Zoology. Two females from Morobe Dt., Mt. Misim (Stevens).



H. O.

Text-figure 71.

Proboscis and palp of *Scaptia flavibarbis*, n. sp.

SCAPTIA FLAVIBARBIS, n. sp.

In the discussion under *S. caliginosa* in my earlier paper (op. cit., p. 134) I pointed out that Schuurmans Stekhoven listed two specimens collected by Wollaston in 1912; that he referred to one of these as Walker's type; and that I failed to understand why he said that the first posterior cell was closed in the type specimen. This was not so in either of the Wollaston specimens before me.

It appears that I had not seen the specimen that he regarded as Walker's type, which has since come to light. It bears a label by Stekhoven "*Erephopsis flavibarbus* Type". Evidently he originally proposed to describe it as new and then decided—erroneously—that it was the type of *caliginosa* Wlk. I have already given an account of the true

type of *caliginosa*, and as this newly discovered specimen is distinct I describe it as new using Stekhoven's manuscript name. Incidentally this specimen does have the first posterior cell closed.

Besides being larger than any other New Guinea *Scaptia*, this species is instantly recognized by a peculiar inflation of the stem of the labium (Text-fig. 71). If only one specimen were available, I would be inclined to regard this as an individual peculiarity, but there is a second specimen from an entirely independent collector. In the key (op. cit., p. 130) this species runs down to *floccosa* Oldr., but is bigger, the palpi are less elongate, the distal wing-band less distinct, and the conspicuous supra-alar tufts of white hairs are absent.

♀. *Head.* Frons and face reddish brown, with yellow-brown tomentum, and rather long black hairs on upper half. Parafacials grey with long black hairs, and a few yellow ones above. Face more brown, with black hairs. Eyes with thick, dark brown pile. Antennae—first two segments brown with black hairs, the following segments bright orange, only a little darker towards tip. Palpi and proboscis as in Text-fig. 71; palpi orange, proboscis black with faint reddish dusting on stem.

Thorax. Mesonotum mahogany-red, with some greyish dusting and short black hairs. Humeral and supra-alar tufts yellow, but not conspicuous as in *floccosa*. Pleura reddish with grey tomentum and yellow hairs, perhaps a few darker ones on mesopleuron.

Abdomen. Dorsally shining mahogany-red, hind margins of segments black, hairs all black. No pale hairs on side margins. Venter similar, rather blacker and hairs longer.

Legs. Fore and middle legs yellow, femora with grey dusting. Black hairs on femora, yellow hairs on tibiae and first tarsal segment. Hind legs brown, with black or brown hairs.

Wings. Basal band well defined, apical band rather faint. Tegular tuft mainly black.

Length. Body 17 mm.; wing 16 mm.

In the British Museum are the holotype female, Upper Utakwa Valley, 5,000–10,000 ft., Feb.–Mar., 1912 (Wollaston), and one female paratype, Wakwa Expedn., Camp iii, 2,500 ft., Dec., 1912 (Boden Kloss).

LIST OF SPECIES OF NEW GUINEA TABANIDAE.

PANGONINAE.

Chrysops albicincta Wulp.

Pareucompsa dimidiata Wulp.

femoralis Ric.

Lilaea atriventer S.S.

de meijerei Ric.

flavicincta S.S.

vittata Ric.

Scaptia albibarbis S.S.

auripilosa Oldr.

bernhardi Oldr.

caliginosa Wlk.

flavibarbis Oldr.

floccosa Oldr.

insularis Oldr.

leonina Oldr.

mafulensis Oldr.

novaeguineensis Ric.

taylori Oldr.

unilineata Oldr.

Chasmia basifasciata de Meij.

bincta End.

Chasmiella brevisculus Wlk.

fasciata Oldr.

fulgidus Ric.

ochrothorax S.S.

papouinus Wlk.

parva Oldr.

parvicallosa Oldr.

raffrayi Big.

subhastata Oldr.

Chalybosoma luciliaeformis S.S.

malkini Oldr.

metallicum Ric.

Cydistomyia albithorax Ric.

doddi Tayl.

aluensis Oldr.

bissecta Oldr.

caesius Wlk.

leucopterus Wulp.

crepuscularis Oldr.

dimorpha Oldr.

festiva Oldr.

heydoni Oldr.

TABANINAE.

Neobolbodimyia nigra Ric.

Japenoides cheesmani Oldr.

Cydistomyia imitans Oldr.
immatura Oldr.
immigrans Oldr.
inopinata Oldr.
laetus de Meij.
lamellata Oldr.
lorentzi Ric.
misimensis Oldr.
nigerrima Oldr.
nokensis Oldr.
oudella Oldr.
pseudimmatura Oldr.
sol S.S.

Tabanus angusticallosus S.S.
angustilineatus Oldr.
approximatus Oldr.
aurivittatus Ric.
ceylonicus Schin.
kershawi Ric.
cinnamoneus Dol.
ceramensis S.S.
cohaerens Wlk.
picticornis Big.
alfourensis Big.
daruensis Oldr.
denticulatus Ric.
divisus Ric.
doreicus Wlk.
sonnerati Big.

Tabanus exagens Wlk.
flammeus S.S.
flavipennis Ric.
furunculigenus Dol.
obscuratus Wlk.
illustris Ric.
indistinctus Big.
infuscatus Oldr.
lenticulatus Oldr.
opalescens S.S.
patriarchus Oldr.
pollinosus Ric.
productus Oldr.
recusans Wlk.
rubriventria Macq.
novaeguineensis Ric.
rufnotatus Big.
designatus Ric.
semicircularis Ric.
serus Wlk.
facilis Wlk.
laglaisei Big.
stüberi Oldr.
truncatus Oldr.
vanleeuweni Oldr.
wollastoni Ric.

The following recorded specimens are of uncertain position:

Tabanus albidosegmentatus S.S.
aroensis S.S.
bipunctatus S.S.
erythrocephalus Wulp.
griseiventer S.S.
latisegmentatus S.S.
olivaceus S.S.
selens S.S.
yulensis v. Roder.

Silvius latistriatus S.S.
atripes S.S.
variegatus S.S.
atratus S.S.

TAXONOMIC NOTES ON THE GENUS ABLEPHARUS (SAURIA: SCINCIDAE).

II. THE RACES OF ABLEPHARUS BURNETTI OUDEMANS.*

By STEPHEN J. COPLAND, B.Sc.

(Plate xxii; twelve Text-figures.)

[Read 27th October, 1948.]

INTRODUCTION.

This second paper on Australian members of the Scincid genus *Ablepharus* Fitzinger deals with the races of *Ablepharus burnetti* Oudemans. The species is recorded, apparently for the first time from New South Wales, about 600 miles south of any previous record known to me. Specimens from this State have been described as members of a new subspecies. The species has been figured for the first time. Notes are given on the nominate race. *Ablepharus heteropus* Garman, which had been relegated to the synonymy of *A. burnetti*, is believed worthy of subspecific differentiation.

ABLEPHARUS BURNETTI SYDNEYENSIS, subsp. nov.

Diagnosis.—*Ablepharus burnetti sydneyensis* is separated from the typical subspecies *A. b. burnetti* by the ear-opening being normally larger and comparatively free of denticulation as well as the other points of difference given in Table 2.

Holotype.—No. 3061 in the author's collection; Mt. Riverview Lookout, near Blaxland, on the eastern scarp of the Blue Mountains, New South Wales (c. 33.44 S., 150.39 E.); 21.v.1946.

Description of Holotype.—Rostral not projecting, smoothly and bluntly rounded when seen from above, the area visible being equal to about half that of the frontonasal; four times as broad as long; short, slightly concave sutures with the nasals; straight, very short ones, about half the length of those with the nasals with 1st supralabials; the very long, slightly concave suture with the frontonasal is almost equal to the width of the frontal. Nasals small, very widely separated, each a rough parallelogram; all sutures rather convex and much the same in length, anterior one with rostral somewhat sinuous, posterior one with anterior loreal, dorsal with frontonasal and ventral, practically straight one, with 1st supralabial, postero-ventral angle touches 2nd supralabial; rounded nostril, with diameter equal to one-third the length of the scale, centrally placed; short groove running back from nostril to posterior border of scale. No supranasals. Frontonasal large, subequal in size to frontal, but noticeably smaller than frontoparietal; very long anterior border against rostral; shorter, sinuous, but nearly straight, lateral border against nasal and anterior loreal, the junction with the latter being about half that with the nasal; long posterior suture slightly concave against most of the prefrontals at sides then scalloped back in the centre against the frontal with which it forms a suture between one-third and one-quarter the width of the latter scale. Prefrontals large, each equal to nearly half the size of the frontal; widely separated; twice as wide as long, somewhat wedge-shaped; long anterior side sinuous and against frontonasal for three-quarters its length and then indented against anterior loreal; posterior border convex for half its length against frontal and then concave against 1st supraocular and 1st supraciliary. Frontal kite-shaped, large, very slightly longer than wide, length equal to its distance from the tip of the snout, width equal to that of the supraocular region at its widest; rather widely in contact with frontonasal anteriorly and frontoparietal posteriorly; sides against prefrontals, 1st and

* For Part I, see these PROCEEDINGS, Vol. lxxi: 282.

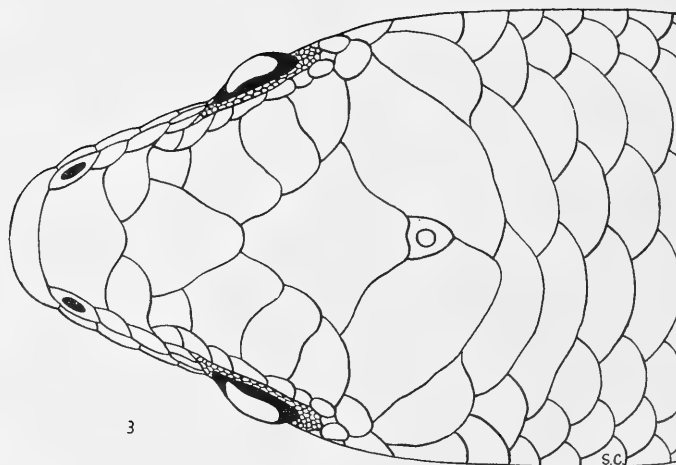
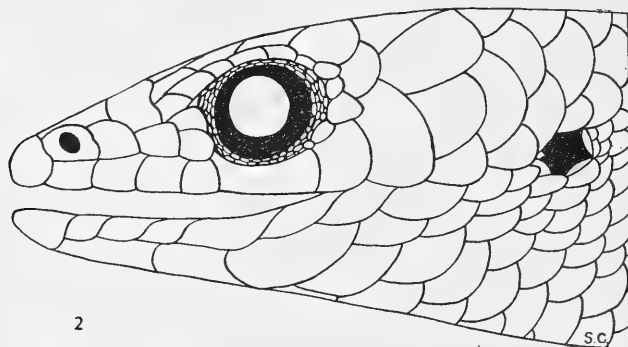
2nd supraoculars; widely separated from 1st supraciliary. Frontoparietal single; considerably longer, wider and larger than the frontal; long, sinuous sutures with parietals; contact with 2nd supraocular somewhat longer than that with 3rd, which is again slightly longer than that with 4th; indented against small kite-shaped interparietal. Interparietal rounded behind and enclosed between parietals, about one-quarter



Fig. 1.—Map showing localities mentioned in this paper.

the length of the frontoparietal; rather indistinct, central, rounded pineal area. Parietals each nearly equal to frontoparietal in size; irregularly lens-shaped, long axes, which diverge at about 90°, twice the length of the short; meeting behind the interparietal in a rather long suture sloping backwards towards the left; other sutures, long, convex, but nearly straight, with nuchal; about same length, or slightly longer, with upper secondary temporal; slightly concave, sinuous and about the same length

with frontoparietal; shorter and distinctly concave with 4th supraocular; and much shorter again with interparietal and 3rd postocular. Two nuchals on left side, one on right, each about twice the width of a following body scale. Seven supralabials, anterior four small, squarish, and not differing greatly in size, though the two end ones are smaller than the two they enclose; 1st in contact anteriorly with rostral and dorsally with nasal; 2nd dorsally with loreals; 3rd dorsally with posterior loreal and shortly dorso-posteriorly with the lower preocular; 4th dorsally with lower preocular; 5th very large, equal in size to three of the anterior supralabials, boat-shaped, long and concave upper margin forming the entire lower margin of the eye; 6th large and squarish, upper margin against a granule, postsubocular and 2nd postocular; 7th by



Figs. 2-3.—Head scales of holotype of *Ablepharus burnetti sydneyensis*, subsp. nov.
2. Dorsal view. 3. Lateral view. Length of head, 6 mm.

far the largest supralabial, being fused so completely with the primary temporal that only one scale is apparent, oblong, long anterior edge against 6th supralabial and 2nd postocular, slightly longer posterior border against secondary temporals and postlabial, shorter upper border against 3rd postocular. Large postlabial is separated by a single scale from the ear opening. Primary temporal indistinguishably fused with 7th supralabial. Upper secondary temporal three times the size of the 3rd postocular, contained between it, parietal, 1st nuchal, a body scale, tertiary temporal, and 7th supralabial. Lower secondary temporal squarish, larger than 3rd postocular, bounded posteriorly by the tall, band-like tertiary temporal. Body scales begin behind the

nuchals, upper secondary temporal, tertiary temporal and postlabial. Anterior loreal slightly smaller than nasal, taller than long, nearly straight anterior and ventral borders against nasal and 2nd supralabial respectively; long, sweepingly convex, dorsal and posterior border against frontonasal, prefrontal and posterior loreal. The posterior loreal is squarish; about equal in size and shape to the anterior; lying between anterior loreal, prefrontal, 1st supraciliary, preoculars, and 2nd and 3rd supralabials. The eye is large and is surrounded by rings of small, elongated granules; for the most part there are three rings of granules showing, but there is some irregularity, additional rows of granules appearing anteriorly and posteriorly, where they become more rounded. Two rather large, squarish preoculars, subequal in size, bound the granules anteriorly, and two small postoculars and a still smaller postsubocular behind. The 3rd postocular is large, about equal in size to half the 4th supraocular, squarish, contained between 4th supraocular, parietal, upper secondary temporal, 7th supralabial, 1st and 2nd postoculars and 7th supraciliary. Of the seven supraciliaries, the 1st and 2nd are largest, subequal in size and roughly squarish; the others are considerably smaller, roughly oblong except for the 7th, which is rounded; the 1st is widely separated from the frontal. There are four well-developed supraoculars, the 2nd by far the largest, then

TABLE 1.

Measurements in mm. and other details of the Holotype, Paratypes and an Auxiliotype of Ablepharus burnetti sydneyensis, subsp. nov.

Number.	A.C. 3061.	A.C. 158.	A.C. 458.	A.C. 809.	A.C. 297.
Snout-vent	32	29	30	29	31
Tail	25	37	30	36	27.5
Snout-ear	6.5	6	6	5.5	6
Snout-forelimb	11	9.5	11	10	11
Axilla-groin	15	14	15	16	17
Head, length	6	6	6	5.5	6.5
Head, width	4.5	4.5	5	5	4.5
Body, width	5.5	4.5	5.5	6	5.5
Forelimb, length	7.5	7	8	8	8
Hindlimb, length	10	10	10	9	9.5
Tail/Snout-vent	0.78	1.28	1.00	1.24	0.89
Axilla-groin/Snout-forelimb	1.36	1.47	1.36	1.60	1.55
Midbody scale rows	24	26	24	24	26
Dorsal scales between parietals and vent	48	48	49	52	49
Lamellae below 4th toe	21	21	19	20	18

the 3rd, 4th and 1st; the frontal is in contact with the 1st and 2nd; the frontoparietal with the 2nd, 3rd and 4th; and the parietal widely with the 4th. The mental is moderate and followed by a postmental about the same size; there are three pairs of chin-shields, the 1st in contact, the 2nd separated by a single scale, and the 3rd by three scales; each of the 3rd chin-shields is elongated postero-laterally. Seven infra-labials, in order of decreasing size, 5, 4, 6, 7, 3, 2, 1.

The ear-opening is rather large, just smaller than the pupil of the eye, irregularly rounded, without definite denticulation except perhaps for one small irregular scale at the extreme anterior angle; two scales separate it from the last supralabial.

Scales are 24 at midbody, dorsally, laterally and ventrally subequal in size. Caudal scales larger; a series of large, transverse subcaudal scales begins six scales behind the vent. Two preanal scales moderately enlarged. Scales from above vent to parietals, 48.

Body rather short and stubby, the distance between the end of the snout and the forelimb is contained about once and a third in the distance between axilla and groin. Limbs moderately developed, forelimb overlapped by hindlimb to wrist when limbs are

addressed. Fingers and toes rather slender. Four fingers and five toes. Lamellar formula for fingers, 9, 11, 14, 9; for toes, 7, 11, 15, 21, 15; lamellae flattened and indistinct for the most part. Blunted tubercles on palms and soles.

The general dorsal coloration is uniform, medium brown on the body to about half a dozen scales before the hindlimbs, then light reddish brown to the tip of the tail; the transition zone of about a dozen scales is flecked, some scales bearing the darker brown of the body and others the lighter brown of the tail. Ventrally, the head, throat and most of the body are whitish; the tail, limbs and medial area of body to about eight scales from vent are pale brown. There are four longitudinal rows of brown dots along the scales of the lower jaw and the ventro-lateral area to the forelimbs. Under the microscope all dorsal scales are shown to be light brown with obscure dark brown reticulations and striping. The anterior spots of the ventro-lateral rows are each composed of scores of tiny brown dots. Both sets of labials are barred vertically in brown and white. There are scattered white flecks laterally from the shoulders to the head.

TABLE 2.

Differences between A. burnetti burnetti and A. burnetti sydneyensis.

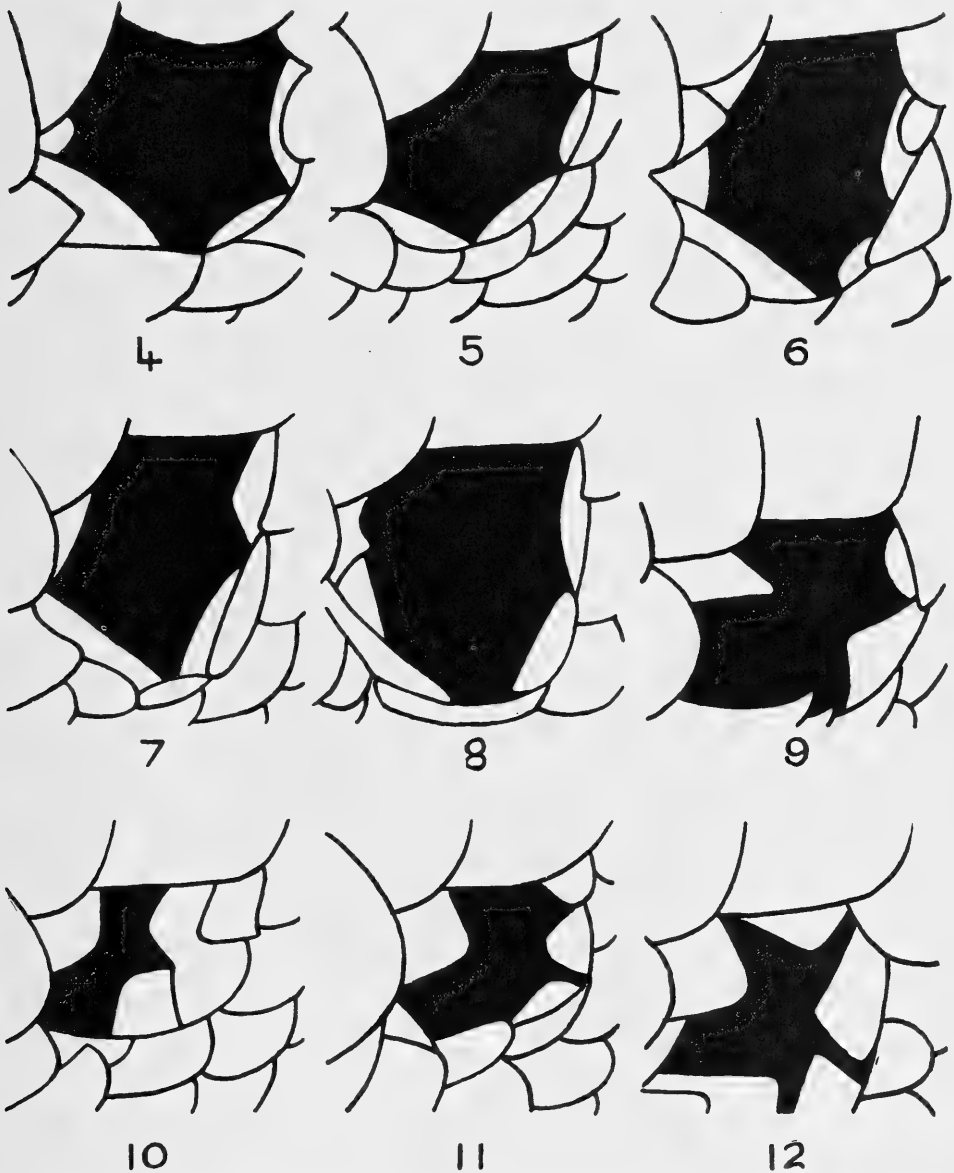
	<i>A. b. sydneyensis.</i>	<i>A. b. burnetti.</i>
Snout	Not projecting.	Slightly, but noticeably projecting.
Length of suture between rostral and frontonasal.	Somewhat narrower than frontal.	Average of seven specimens, 0.19 width of frontal.
Length of suture between frontonasal and frontal.	Between $\frac{1}{2}$ and $\frac{1}{4}$ the width of frontal.	Much narrower.
Anterior loreal in contact with postero-lateral angle of 1st supralabial.	No, in two specimens; at point in two.	Yes, in five specimens; at point in two
Size of postmental to mental.	From about equal to half as big again.	Tendency to be about twice the size.
Ear-opening	Just smaller than pupil of eye, almost clear of denticulation, at most one denticulation in specimens examined. See notes in description of holotype and discussion on variation in paratypes, also text-figures 4-8.	Normally smaller and with denticulation much more pronounced: A.C. 570 and A.C. 575, opening about half size of pupil, not rounded, oblique, one anterior and two posterior denticulations; A.C. 577, no denticulation, but opening almost completely closed and appearing as a very small slit; A.C. 598, opening would be practically size of pupil, but is nearly closed by five, large denticulations, A.C. 576, as A.C. 598, but denticulations not so big and opening only half size of pupil; A.C. 574, small, vertical slit with two posterior denticulations; A.C. 590, opening very small with two posterior denticulations. See also text-figures 9-12.

I have named the southern race *sydneyensis* because of its occurrence in the Sydney area.

Paratypes.—In author's collection: Nos. 158, 1 mile from Upper Colo towards Putty, 9.x.1938; 458, 7 miles north of St. Albans on Singleton Road, 1.x.1939; 809, 1 mile north of Parramatta, 24.xi.1940; all localities in New South Wales.

Variation in Paratypes.—The suture between rostral and frontonasal in all three specimens is somewhat narrower than the frontal. A deep groove from the posterior margin of the nasal to the nostril and then to the ventral margin practically divides the nasal in A.C.458. The interparietal is always small, but rather irregular in its proportions, the length varying from twice to equal the width. A.C.158 has two nuchals on each side; A.C.458 two on the left and one on the right; and A.C.809 one

on the left and two on the right. In no case is the 7th supralabial fused with the primary temporal as in the holotype; the 6th is the largest supralabial, and the 7th is pentagonal, considerably smaller than the 6th and about equal in area to the primary



Figs. 4-12.—Ear-openings of *Ablepharus burnetti*. Nine of the 13 specimens discussed have been drawn to illustrate the characteristic differences in size and prominence of denticulation in two races. All figures are drawn to the same scale. 4-8, *A. b. sydneyensis*; 9-12, *A. b. burnetti*. 4, A.C.3061; 5, A.C.158; 6, A.C. 458; 7, A.C.809; 8, A.C. 297; 9, A.C.837; 10, A.C.570; 11, A.C.577; 12, A.C.598.

temporal; it lies between the 6th supralabial, primary temporal, lower secondary temporal and postlabial. The 1st postocular may be reduced to little more than a granule, the 2nd is always prominent, and the 3rd may be very large. Each paratype has six supraoculars. The 3rd and 4th supraoculars are subequal in size in all three

specimens. In A.C.158 a large anterior scale appears as a definite denticulation; A.C.458 has one small anterior denticulation; there is no trace of denticulation in A.C.809. A.C.458 and A.C.809 have the short, sturdy habitus of A.C.3061, but A.C.158 is much thinner and more elongated. All paratypes agree substantially in colour with the holotype. They have the same warm brown dorsally, A.C.158 being slightly darker. A.C.458 and A.C.809 have orange or reddish tails. Measurements and some other details are given in Table 1.

A.C.297, collected 10 miles east of Singleton, N.S.W., 4.iii.1939, is regarded as an auxilotype as defined by Copland (1946, p. 69). There is no doubt that the specimen belongs to the southern race, with the holotype of which it agrees almost exactly, but it has been thought advisable to restrict paratypes to a small area.

The main points of difference between *A. burnetti burnetti* and *A. burnetti sydneyensis* are set out in Table 2.

I have been unable to find any reference to the occurrence of *Ablepharus burnetti* in New South Wales. This is rather surprising because the small lizard, although never occurring in large colonies, appears to have a reasonably widespread distribution. It probably occurs sparingly in suitable habitats on the Blue Mountains north of Sydney and then along the Western Slopes to Queensland. I suspect that it has been taken, but referred to *Ablepharus greyii* (Gray). This would be done by anyone relying on Boulenger's key (1887, p. 345), which was published seven years before Oudemans described his species. *Ablepharus greyii* can readily be distinguished by the number of supraoculars, the large size and band-like appearance of the anterior supraocular, other cephalic scalation, ear-opening, number of midbody scale rows, proportions, habitus and coloration among other characters.

The little lizards are diurnal but secretive in their habits and are rarely seen in daylight unless their cover is disturbed. They hunt under and among the fallen leaves and mould in tree-shaded rather moist places and under the overhang of fallen trees and logs lying in grass and other vegetation in more open situations. A.C.3061 was found in leaves and mould at the side of an overhanging stone between trees typical of the Hawkesbury Sandstone plateau. The sandy soil was slightly moist. A.C.158 and A.C.458 were collected on hillsides above swamps, one under a stone and the other under a log. A.C.297 was under a log in a large, almost cleared paddock. A.C.809 was hidden in mould under a flat stone in coarse sandy soil.

ABLEPHARUS BURNETTI BURNETTI Oudemans.

Ablepharus burnetti Oudemans, 1894, p. 145.

Ablepharus burnettii Zietz, 1920, p. 221.

The seven topotypes of the nominate race I have examined agree completely with Oudemans' original description (1894, p. 145), which follows:

"Burnett River, 4 Ex. Diese Art findet ihren Platz neben *Ablepharus greyi* Gray. Kopf klein, Schnauze kurz und stumpf, Rostrale nicht vorspringend. Auge ganz von granularen Schuppen umgeben. Frontonasale viel breiter als lang, in Contact mit dem Rostrale und dem Frontale, die erste Commissur sehr breit. Frontale fast ebenso lang wie das Frontoparietale, aber weniger breit, in Contact mit den vorderen zwei Supraocularia. Praefrontalia halb so gross wie das Frontale, grösser als das Interparietale. Frontoparietalia verschmolzen. Vier Supraocularia, das zweite am grössten. Vier Labialia vor dem Suboculare. Ein Paar Nuchalia (bei einem Exemplare rechts zwei hinter einander). Ohröffnung klein, rund, mit verschiedenen kleinen Lobuli. 24 bis 26 flache Schuppen rings um den Körper. Zwei etwas grössere Praeanalia. Beine kurz, die vorderen mit 4, die hinteren mit 5 Zehen. Drückt man die Beine gegen den Körper an, so berühren die Zehen von Vorder- und Hinterfuss einander. Schwanz bei allen mir vorliegenden Individuen verletzt, ziemlich dick. Oben dunkelbraun, unten bläulich-weiss."

Oudemans' measurements are given in Table 3.

Specimens Examined and Locality Records of Ablepharus burnetti burnetti.

1 (A.C. 570) 3 mi. from Mundubbera on Gayndah Road, Q., 9.xi.1939.

4 (A.C. 574-7), 30 mi. S. of Mundubbera on Brovinia Station Road, Q., 9.xi.1939.

1 (A.C. 590) 15 mi. from Gayndah on Mundubbera Road, Q., 10.xi.1939.

1 (A.C. 598) 16 mi. S. of Gayndah, Q., 11.xi.1939.

1 (A.C. 837) 2.5 mi. N.E. of Nullamanna, N.S.W., 7.xii.1940.

The first seven specimens taken in the Burnett River valley are topotypes

TABLE 3.

Measurements in mm. and other details of specimens, including *Holotype* and seven *Topotypes*, of *Ablepharus burnetti burnetti*.

Number.	*	A.C. 570.	A.C. 574.	A.C. 575.	A.C. 576.	A.C. 577.	A.C. 590.	A.C. 598.	A.C. 837.
Snout-vent	28	31	32	31	31	32	28	29	27.5
Tail	20†	45	20†	18†	30†	22†	30†	31†	32†
Snout-ear	—	6	6	6	6.5	6.5	5.5	6	6
Snout-forelimb	—	10	11	11.5	11.5	10	10	9.5	10
Axilla-groin	—	17	18	15	16	17	15	15	15
Head, length	6	6.5	6.5	6.5	7	7	6	6.5	6.5
Head, width	4	4.5	5	5	5	5	4	4	4.5
Body, width	—	5	6	6	6	6	5	6	5.5
Forelimb, length	8	7.5	7.5	8	8	7.5	7	7.5	7
Hindlimb, length	10	10	10	10	10.5	10.5	9.5	9.5	9
Tail/Snout-vent	—	1.45	—	—	—	—	—	—	—
Axilla-groin/Snout-forelimb	—	1.70	1.64	1.30	1.39	1.70	1.50	1.58	1.50
Midbody scale rows	24 or 26	24	24	24	24	24	24	24	24
Dorsal scales between parietal and vent	—	49	47	49	48	45	48	50	48
Lamellae below 4th toe	—	17	19	20	19	20	18	20	19

* Measurements from Oudemans' type description. He only gives the one set of measurements—probably taken from the largest of his four specimens.

† Mutilated, more or less regenerated.

The following notes are additional to those of Table 2 or summarize measurements of Table 3. All seven topotypes of *A. b. burnetti* have 24 midbody scale rows. Lamellae under the fourth toe number 17 (one specimen), 18 (1), 19 (2), and 20 (3). The interparietal is abnormally fused with the right parietal in A.C.575. A.C.590 has the suture between the parietals sloping backwards towards the right. Nuchals are most irregular, one specimen having three on each side, 3/3; one, 2/2; one, 2/1; two, 1/2; one, 1/1; and one, 1/0. The average number of lamellae below the fourth toe, *A. b. sydneyensis* 19.8 and *A. b. burnetti* 19.0, and number of scales between the parietals and vent, 49.2 and 48.0 respectively, suggest a shortening of the hindlimbs and body as we proceed northward, though the small number of specimens available does not allow of statistical treatment.

A New South Wales specimen, A.C.837, collected near Nullamanna, almost exactly half-way between the type localities of *A. b. sydneyensis* and *A. b. burnetti* is, as might be expected, somewhat intermediate in its characters. It approaches *A. b. sydneyensis* in the long suture between rostral and frontonasal (it is considerably wider than the frontal), and in not having the snout even slightly projecting. The ear-opening agrees closely with *A. b. burnetti* in the prominent denticulations, but the size of the opening is intermediate between that of the small northern and large southern forms. These features are evident in Fig. 9 and may be compared with the accompanying figures. In all other characters A.C.837 agrees with typical *A. b. burnetti*.

Zietz (1920, p. 221) records *A. burnetti* only from Queensland. *A. b. burnetti* appears to be less secretive in its habits than the southern race. The seven topotypes dealt with here were all collected while hunting or resting beside or under logs, six being in partly cleared paddocks and A.C.590 on a dry, stony hillside. The Nullamanna specimen was found under bark and fallen branches.

Possibly the less secretive habits of *A. b. burnetti* may explain the fact that Oudemans' specimens and seven of the eight lizards I have collected have damaged tails, whereas all five tails of *A. b. sydneyensis* are apparently intact.

ABLEPHARUS BURNETTI HETEROPUS Garman.

Ablepharus heteropus Garman, November, 1901, p. 9; Zietz, 1920, p. 221.

Ablepharus burnetti Loveridge, 1934, p. 378.

Ablepharus heteropus is not represented in the collections of the Queensland Museum and, being unable to obtain a specimen for examination, I have had to rely on Garman's type description. A detailed comparison of this with Oudemans' description and with topotypes of *A. b. burnetti* in my possession leaves no doubt that the Great Barrier Reef and Burnett River forms are conspecific. The comparison, however, brings out apparent differences, which seem to justify subspecific recognition of Garman's form.

Garman's original description (1901, p. 9) follows:

"Head medium; snout short blunt, rounded, slightly rojecting. Eye surrounded by granules. Rostral slightly swollen, largely in contact with the frontonasal; frontal moderate, hexagonal, in contact with frontonasal, interparietal,* prefrontals, and two anterior supraoculars. Prefrontals about half as large as the frontal, not in contact. Frontoparietal large, much larger than the frontal. Interparietal distinct, small, hardly as large as a prefrontal. Four supraoculars, anterior smallest, second largest. Labials six, fourth long and below the orbit. Parietals broad, in contact behind the interparietal. Two pairs of broad nuchals. Ear opening small, nearly hidden by sharp lobules from the upper and the lower edges. Scales smooth, in twenty-four rows around the body, scales of flanks smallest. Preanals small. Limbs short, anterior tetradactyl, posterior pentadactyl, not meeting when adpressed. Digits short, outer on the hind foot very short. Tail longer than head and body. Brownish olive above, lighter toward the belly, with small spots of brown below the hinder part of the abdomen, under the tail, on the limbs, along the lower edges of the flanks, and on the lips and the sides of the throat; belly, throat, and lower surface of tail white. Near *A. Greyi* Gray, of Western and Southern Australia. Great Barrier Reef, Queensland; G.B.R. Exp."

The points of difference between *A. b. heteropus* and *A. b. burnetti* are set out in Table 4.

TABLE 4.

Differences between A. b. heteropus and A. b. burnetti.

	<i>A. b. heteropus.</i>	<i>A. b. burnetti.</i>
Rostral	Slightly swollen.	Not swollen.
Interparietal	Hardly as large as a prefrontal.	Half size of prefrontal.
Supralabials	Six, fourth below orbit.	Seven, fifth below orbit.
Ear-opening	Small, nearly hidden by sharp lobules from the upper and the lower edges.	Intermediate between <i>A. b. heteropus</i> and <i>A. b. sydneyensis</i> ; normally not large, but not "nearly hidden".
Length of limbs	Not meeting when adpressed.	Meet or overlap slightly.
Colour	Small spots of brown below the hinder part of the abdomen, under the tail, on the limbs, along the lower edges of the flanks, and on the lips and the sides of the throat.	Spots generally missing except on lips. Occasional spot on limbs and in sub-lateral position. Spots a most inconspicuous feature.

There is a progressive comparative shortening of the limbs (overlapping to wrist: meeting or overlapping slightly: not meeting when adpressed), decrease in the size of the ear-opening, and increase in the prominence of denticulation as we proceed northward from *A. b. sydneyensis*, through *A. b. burnetti*, to *A. b. heteropus*. Tables 2 and 4 taken together exemplify this and other trends.

* Lapsus for frontoparietal.

Loveridge (1934, p. 378) synonymizes *Ablepharus heteropus* with *A. burnetti*. He had only a single specimen at his disposal (Museum of Comparative Zoölogy, No. 6486); Garman's holotype of *heteropus* from the Great Barrier Reef, collected by the Barrier Reef Expedition in 1896; and no comparative material of *burnetti*. He gives the total length of the holotype, which was omitted in the original description, as 57 (26 + 31) mm.

Zietz (1920, p. 221), in his catalogue, gives only Garman's locality record.

ACKNOWLEDGEMENTS.

I wish to thank Professor W. J. Dakin and Professor E. A. Briggs, of the University of Sydney, and Dr. A. B. Walkom, Mr. J. R. Kinghorn and Mr. W. A. Rainbow, of the Australian Museum, for help and encouragement. Mr. George Mack, of the Queensland Museum, kindly searched his collections for specimens without success. Miss A. G. Burns, of the Department of Zoology, University of Sydney, is again to be thanked for the photographs.

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EXPLANATION OF PLATE XXII.

Fig. 1.—Dorsal view of holotype of *Ablepharus burnetti sydneyensis* (A.C.3061).

Fig. 2.—Lateral view of same specimen.

Length of head and body, 32 mm.

Photos.—Miss A. G. Burns.

REVISIONAL NOTES ON AUSTRALASIAN SIMULIIDAE (DIPTERA).

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Queensland Institute of Medical Research, Brisbane.

(With twenty Text-figures.)

[Read 27th October, 1948.]

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INTRODUCTION.

The time is not ripe for a full monographic treatment of the Australasian Simuliidae—too many life histories are still unknown; but we are stimulated to offer these notes, because we have had the opportunity to re-examine Tonnoir's extensive collection in the Division of Economic Entomology, C.S.I.R., and because Smart's (1945) revision has provided a basis on which the genera in the region may be reviewed. Moreover, our fauna presents anomalies which make Smart's definitions difficult to follow in some respects, so we feel that it would be helpful to discuss these problems now.

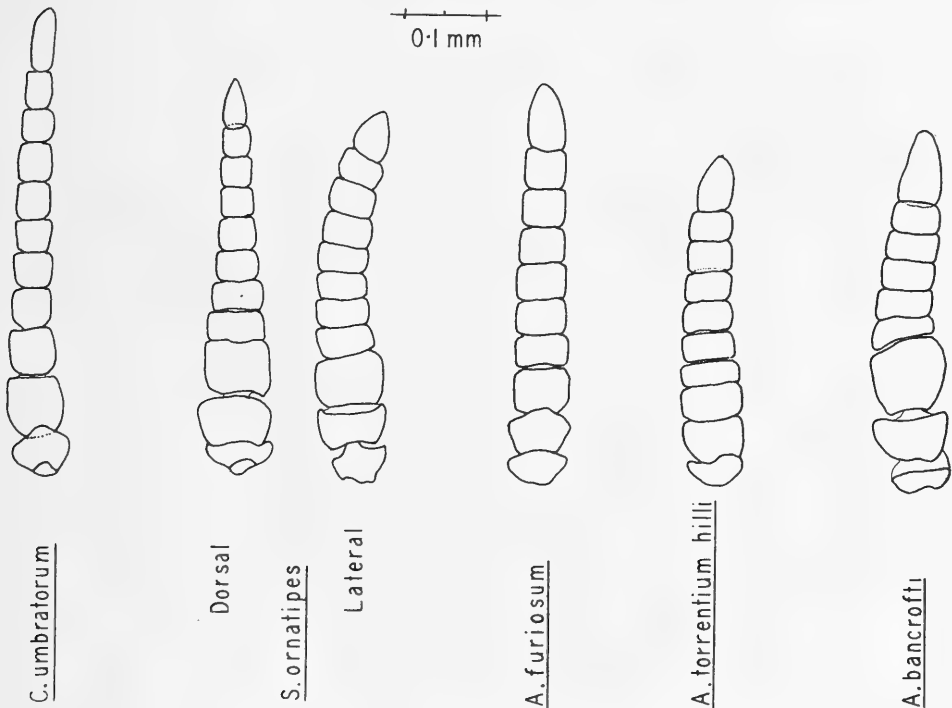
The Australasian fauna, as at present known, comprises 20 species and three subspecies from Australia and Tasmania, four species from New Guinea, and seven from New Zealand. The New Guinea species all belong to *Simulium*, as restricted by Edwards (1931, 1934) and Smart (1945), those from New Zealand are all *Austrosimulium*, and three genera are represented in Australia.

Tonnoir (1925) contributed most largely to our knowledge, later systematic papers being by Taylor (1927) on two species from Queensland, Drummond (1931) on the Western Australian species, Wharton (1948) on those from New Guinea, and the writers (1948) on those from Queensland. Enderlein (1922, 1936) had recorded three species from New Guinea. Edwards (1931, p. 131) transferred three of the Australian species of *Simulium* (*aurantiacum* Tonn., *terebrans* Tonn. and *umbratorum* Tonn.) to *Cnephia*, which was followed by Smart in his catalogue.

In the present paper, we propose to re-define the genera, record synonymy, give descriptive notes of the known species, and indicate the directions in which immediately profitable work might be undertaken. We consider that it does not help other workers at the present day to describe new species on adults only, and therefore only indicate certain forms by letters. It has, however, been necessary to refer to two of Tonnoir's MS. names, because the types were labelled and placed in the collection of the School of Public Health and Tropical Medicine, Sydney, before his death; both of these names are preoccupied.

As regards types, only the location of the holotype is mentioned, unless there is reason to refer to other types also.

This revision has been made possible, because Tonnoir's collection, including his undescribed material, was made available to us through the kindness of Dr. A. J. Nicholson, Chief of the Division of Economic Entomology, C.S.I.R., Canberra. We have also had access to Tonnoir's notes, and have been able to use them in places indicated in the text. In addition, we have received help with specimens and information from Messrs. T. G. Campbell, C.S.I.R., Canberra; K. J. Clinton, School of Public Health and Tropical Medicine, Sydney; R. H. Wharton, Department of Zoology, University of Sydney; A. R. Woodhill, Lecturer in Entomology, University of Sydney; and D. Mackerras, Sydney. To all of these, we express our thanks, especially to Mr. Wharton, for permission to use his undescribed material.



Text-fig. 1.—Antennae of females, showing range of variation.

Our thanks are due also to the Editor of the *Australian Journal of Scientific Research* for permission to incorporate elements from our earlier paper to complete some figures in the present work, and to the Editor of the *Bulletin of Entomological Research* for allowing us to use two figures of *A. cornutum* from Tonnoir (1925). As a result of their consideration, it should be possible for workers to identify all the known Australian "gill-spot" larvae and pupae from the illustrations given here.

We can only regret that our old friend, A. L. Tonnoir, did not survive to undertake this revision himself.

MORPHOLOGY.

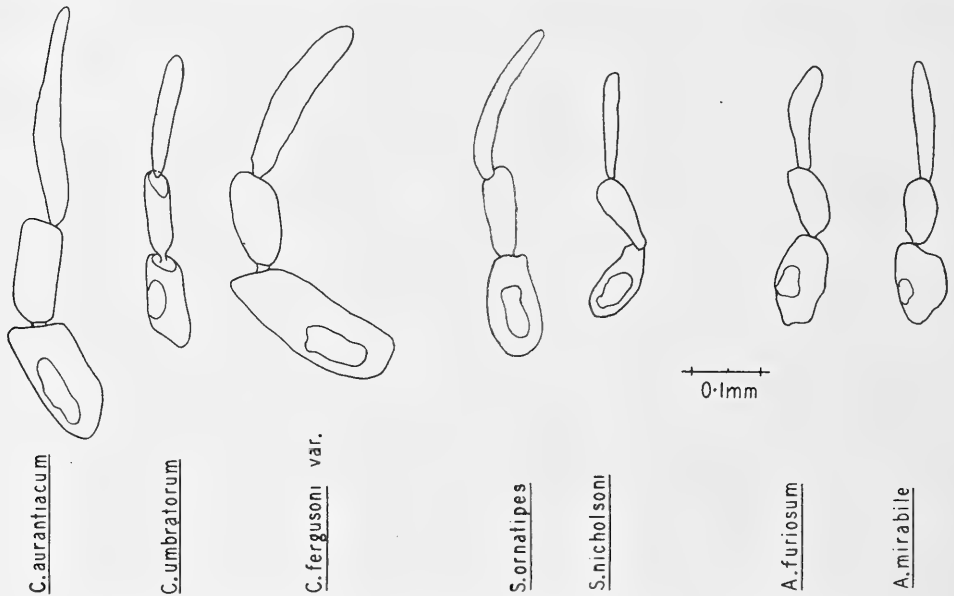
Apart from the extremely aberrant *Parasimulium* Mall., Edwards (1931) recognized seven subgenera of *Simulium*, five of which Smart (1945) restored to generic rank, namely: *Prosimulium* Roub. (Holarctic), *Cnephia* End. (Holarctic, Neotropical, Australian), *Gigantodax* End. (Neotropical), *Austrosimulium* Tonn. (Neotropical, Australian), and *Simulium* Latr. (cosmopolitan). The first three are obviously closely

related to one another, and seem to represent a line of evolution distinct from the rest of the family. *Austrosimulium* is also a compact group; its relationships are obscure, but appear to lie rather with the *Prosimulium* complex than with *Simulium*. *Simulium* itself is probably polyphyletic, though there are some features common to the species, which suggests that, as a whole, it represents a third main line of evolution in the family.

These three lines are, for the most part, well indicated in the structure of the pupae and cocoons, but the adults are less clearly separated, and the larvae scarcely at all. We have examined the Australian species to see whether they help or hinder solution of the problem of relationships, and present our notes below in order to avoid needless repetition in the generic definitions.

ADULTS.

Head: The antennae (Fig. 1) are eleven-segmented in *Cnephia* and *Simulium*, ten-segmented in *Austrosimulium* (except *A. bancrofti*, which has nine-segmented antennae). The number of segments is constant in every species we have examined. The terminal segment of the palp (Fig. 2) is long in some *Simulium* and the *aurantiacum* group of *Cnephia*, short in *Austrosimulium*, and short or intermediate in the *terebrans* group of *Cnephia*. There is considerable variability, and the taxonomic value of this character is limited. The upper eye-facets of the male are unusually enlarged in some species of the



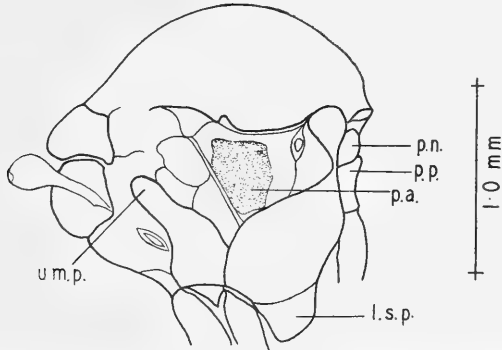
Text-fig. 2.—Distal three segments of palpi of females, showing range of variation.

clathrinum group of *Simulium*, but not in all, and this character has a limited value in suggesting relationships of obscure species (e.g., *S. oculatum* End.). We have not studied the bucco-pharyngeal armature.

Thorax: The scutum is strikingly humped in the *aurantiacum* group, normal in all other members of the family. The general pubescence is short, fine, and appressed in *Cnephia* and *Austrosimulium*, denser and with a stronger tendency for the hairs to develop into lanceolate scales in *Simulium*. As regards the pleural chaetotaxy, anterior pronotal and upper mesepimeral hairs are present in all species. Propleural hairs are present and conspicuous in all species of *Simulium*, usually absent in *Cnephia* (their presence in *C. aurantiacum* is a good specific character), and quite inconstant in *Austrosimulium*, even within some of the species. The possession of a conspicuous patch

of scales on the membranous area anterior to the wing-root and lower sternopleural* hairs sharply distinguishes the *clathrinum* group of *Simulium* from all other Australasian members of the family. The areas referred to are shown in Figure 3.

Wings: Edwards (1931) indicated the importance of stouter spinules among the hairs on the costa, and a study of this character in the Australian material has given interesting results. *C. fergusonii* Tonn, apparently completely lacks spinules, and so its wing is separable from that of *Prosimulium* only by the unforked Rs. In *C. aurantiacum* spinules are present, but poorly differentiated. They are better developed in the remaining species of *Cnephia* and in *Austrosimulium*, but are especially conspicuous and thorn-like in *Simulium*. Of greater local importance is the presence of similar spinules among the hairs on the upper surface of R₁ in all the species of *Simulium*, and their absence in both the other genera.



Text-fig. 3.—Lateral view of thorax of female *C. aurantiacum*. p.n. Anterior pronotal lobes. p.p. Propleuron. p.a. Membranous prealar area. l.s.p. Lower sternopleural area. u.m.p. Upper mesepimeral area. (Hairs omitted.)

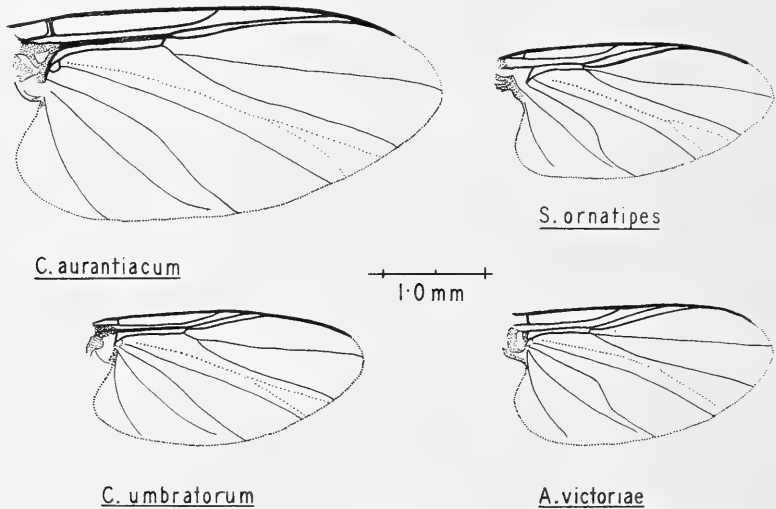
Sc is haired below in all species; R (usually referred to as basal section of radius) haired above in all, except one aberrant member of the *clathrinum* group; R₁ haired above in all; R_s haired below throughout its length, and above on its distal section, in all species. In *Cnephia* and *Austrosimulium* the hairs on the upper surface of R_s commence about opposite the tip of R₁; in *Simulium* they are practically restricted to the distal end, where R_s comes into apposition with costa. *A. mirabile* is aberrant in having the hairs on the veins largely concentrated in tufts.

The small cell at the base of the wing (Edwards, 1931) is sometimes difficult to see, but is indicated in all species of *Cnephia* and *Austrosimulium*, absent in *Simulium*. Cu₂ is gently sinuous in the *aurantiacum* group of *Cnephia*, almost straight in *C. umbratorum*, and with a strong double curve in all other members of the family (Fig. 4). This last character, though a relative one, seems to be a useful taxonomic feature of the wing.

Legs: We have not been impressed with the chaetotaxy of the legs or the form of tibiae and metatarsi as assisting in generic or group recognition, though the very long hairs described by Enderlein on the fore tarsi seem to be rather characteristic of the *clathrinum* group. A calcipala is present in all species except in the eastern form of *C. fergusonii*, though it is indicated in the Western Australian race. It is particularly large and conspicuous in *C. aurantiacum* and its allies. Similarly, the pedisulcus is well defined in *Simulium* and *Austrosimulium*, present but shallow in most *Cnephia*, and absent only in the two races of *C. fergusonii*. Teeth on the female claws may be present or absent in all three genera, and so (as both Edwards and Smart have pointed out) have little taxonomic value for major groupings. Most males have the peculiar untoothed claws figured by Tonnoir, but a few (e.g., *A. crassipes*, *A. victoriae*) have a minute basal tooth.

* This is the area called mesosternal by Edwards (1934); but it corresponds with the lower sternopleural area of other groups, and is clearly divided by a median, ventral suture, which is curious for a sternal plate.

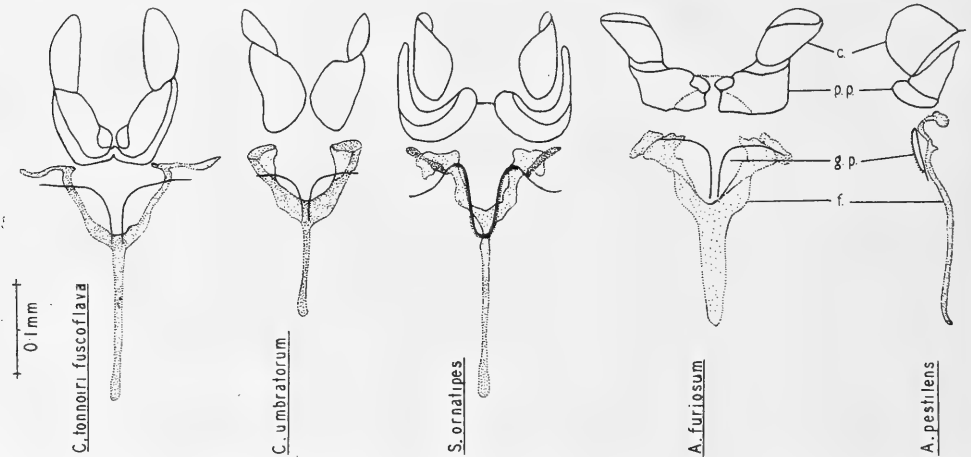
Abdomen: The abdomen is strongly hirsute in the *aurantiacum* group, densely covered (at least over the greater part of the dorsum) with scales in *Simulium*, and relatively bare in *Austrosimulium* and the *terebrans* group of *Cnephia*. These features, in combination with the general pubescence of the thorax and legs, give the several



Text-fig. 4.—Wings of females, showing variation of Cu_1 and small cell.

groups quite distinctive appearances, so that an insect can be placed with considerable accuracy by means of a hand-lens alone.

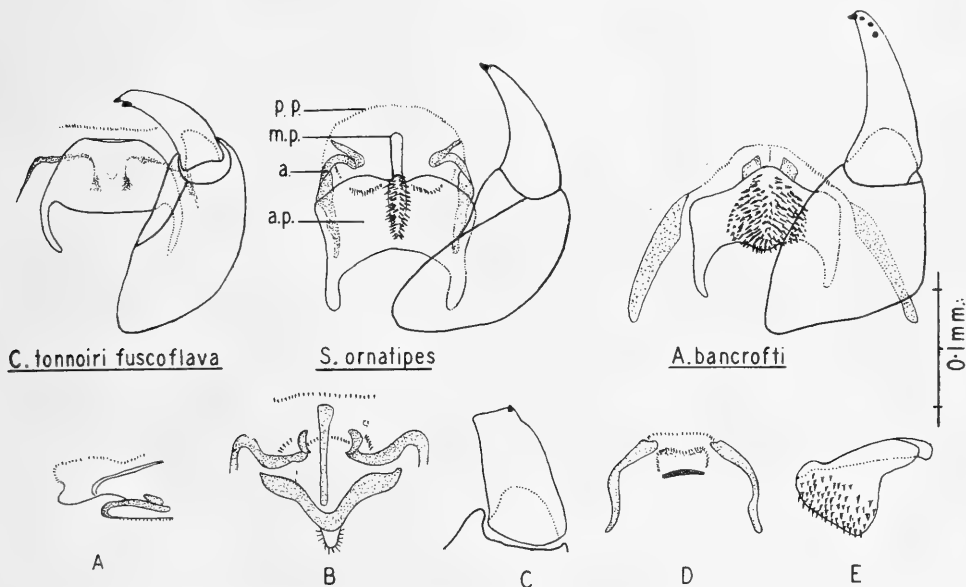
Female genitalia: An examination of these structures was disappointing. There were differences between species (which could be recognized as easily by more accessible characters) but few between groups. The anterior gonopophyses are mostly delicate,



Text-fig. 5.—Genitalia of females. c. Cerci. p.p. Paraprocts. g.p. Anterior gonopophyses. f. Genital fork. (Terminology after Gibbins, 1934.)

but are strongly chitinized in *S. ornatipes* (giving the appearance of a “cleft sternite”), and to a lesser degree in some of the darker species of *Austrosimulium*. The paraprocts (basal segment of cercus of Mackerras and Fuller, 1942), generally triangular or quadrate, are elongate in the *aurantiacum* group, and fused basally in the midline in

C. tonnoiri fuscoflava. The cerci are more or less semilunar lobes in lateral view in nearly all the species, and the tenth segment is small and lightly chitinized in nearly all. The genital fork alone showed useful differences, its stem being relatively long and slender in dorso-ventral view in *Simulium*, shorter and broader in *Austrosimulium*. The *aurantiacum* group of *Cnephia* corresponded to *Simulium*, but the *terebrans* group tended to be intermediate, in that the stem was relatively short though slender. *C. aurantiacum* is the only species we have seen with a strongly sculptured spermatheca.



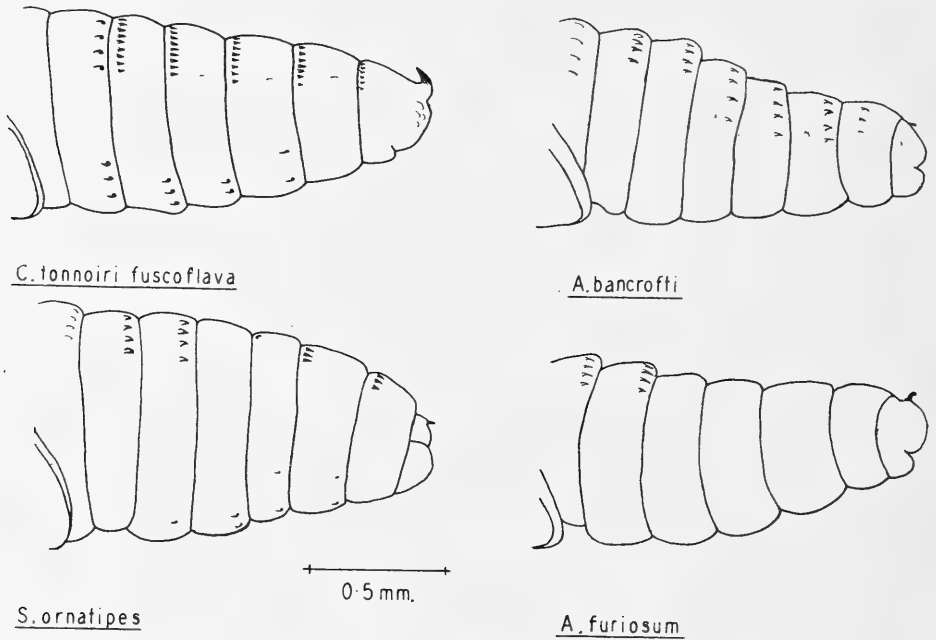
Text-fig. 6.—Genitalia of males. p.p. Posterior part of phallosome. m.p. Median piece. a. Apodeme. a.p. Anterior part of phallosome. Lower row: A. Sagittal sectional view of phallosome of *C. tonnoiri fuscoflava*. B. End view of phallosome of *S. ornatipes*. C. Internal view of style of *S. ornatipes*. D. Dorsal view of posterior part of phallosome and apodemes of *S. clathrinum*. E. Lateral view of anterior part of phallosome of *A. bancrofti*. (Terminology after Gibbins, 1935.)

Male genitalia: These also were not as useful as might have been expected. Nevertheless the number of spines on the style differ in the genera (Fig. 6), and the ventral surface of the anterior part of the phallosome (Gibbins, 1935) is swollen and coarsely setulose in *Austrosimulium*, whereas it is more nearly flat and smooth in the other genera. The most distinctive and complex hypopygium is possessed by *S. ornatipes*, which has, not only a median, setulose, ventral keel on the anterior part of the phallosome, but powerful apodemes, and well developed structures on the posterior part. This is the only species with a clearly defined, heavily chitinized median process, though the presence of one is indicated also in a few species of *Austrosimulium*. The style is longer than the coxite in only one species (*A. bancrofti* Tayl.). When we come to *A. furiosum* and its relatives, the males of which cannot be separated satisfactorily on external characters, we find that, while there do appear to be differences in the number and arrangement of the denticles on the posterior part of the phallosome, these parts are so difficult to see, and errors due to position and distortion are so likely that they have little practical value.

PUPAE.

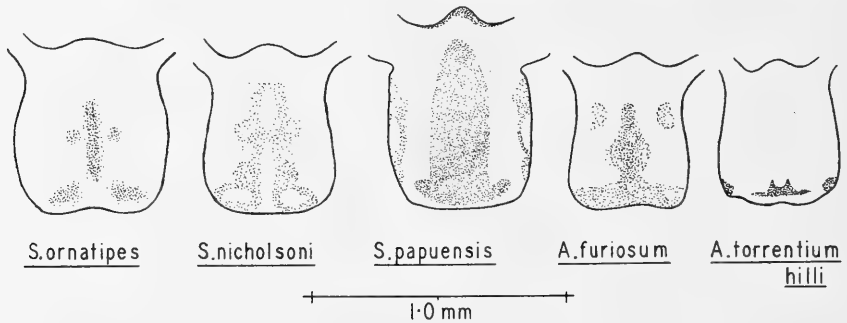
The pupae offer, not only the best specific characters, as Tonnoir (1925) pointed out, but the best generic characters, too, the most useful being found in the form of the thoracic respiratory organs and the abdominal armature of strong spines and hooks

(Fig. 7). These features are described below in the definitions of the genera, but it may be remarked here that we would have been doubtful of the wisdom of recognizing *Cnephia* as a distinct genus in the Australian fauna, if it were not for the relationship



Text-fig. 7.—Representative pupae. Lateral view of abdomen, showing armature.

shown by the known pupae and cocoons to *Prosimulium* and its allies. *Simulium papuense* Wh. is unusual, in that the respiratory organs are of arborescent *Prosimulium* form, whereas the abdominal chaetotaxy is typical of *Simulium*.



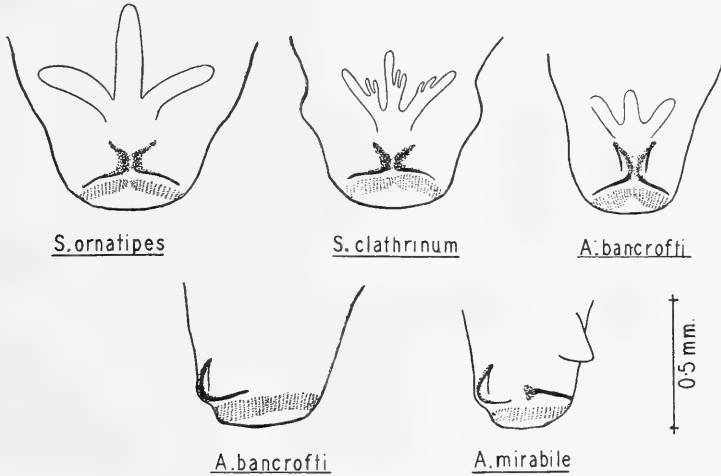
Text-fig. 8.—Heads of larvae, showing variation in pattern.
(For *papuensis* read *papuense*.)

LARVAE.

The larvae are rather uniform, and we have only found two characters which correlate with groupings based on pupae and adults. The backwardly directed strut in the anal armature (Fig. 9) occurs only (and constantly) in *Austrosimulium*, and the form of the pupal gill-spot varies in the three genera (Fig. 19).

It is apparent that *Austrosimulium* is well differentiated in all stages, even the cocoons being recognizable generically by their failure to enclose the abdomen of the pupa ventrally. The cocoons also distinguish *Cnephia*, perhaps better than any other

feature, but the abdominal chaetotaxy of the pupa, too, is distinctive. Other characters separating *Cnephia* from *Simulium*, unfortunately, are relative, or show exceptions, like the pupal gills of *S. papuense* or the propleural hairs of adult *C. aurantiacum*, so that their usefulness is correspondingly impaired. Nevertheless, when they are treated collectively, and when obvious inter-specific relationships are taken into account, too, the groups do appear natural, and give the impression that they can be accepted with reasonable confidence.



Text-fig. 9.—Terminal segments of larvae; top row: dorsal view, showing anal sclerite and rectal gills; bottom row: lateral view, showing ventral papillae and chitinous ring in *A. mirabile* and their absence in *A. bancrofti*.

DISTRIBUTION.

The species of *Cnephia* are typically "Antarctic" in distribution, occurring in Tasmania and the south-eastern highlands of the mainland, with extensions to south-western Australia and to Stradbroke Is. in Queensland. Their relationships, too, obviously lie with the *Prosimulium* complex, which radiated widely in the Andean sub-region of South America, where it is represented by the genera *Cnephia* and *Gigantodax*.

Austrosimulium is also a southern genus, well represented in Tasmania, but extending more widely on the mainland than *Cnephia*, and showing a capacity to thrive in semi-arid, inland country. Its affinities are obscure, but its "Antarctic" origin is clear from the occurrence of species in New Zealand and South America.

On the other hand, *Simulium ornatipes* is a typical *Eusimulium* with Austro-Malayan affinities, and the members of the *clathrinum* group belong to the same zoogeographical element, being distributed in the northern half of the continent and New Guinea, and finding their nearest relationships with Edwards' (1934) Group C from Java and Sumatra. It is of considerable interest that such a small and specialized group as the Simuliidae should present in miniature so much of the zoogeographical picture of the Australian fauna as a whole.

As regards species, it has become clear that many are much more widely distributed than Tonnoir imagined (Table 1). *S. ornatipes* is the outstanding example, for it extends from Perth right through the eastern States and into New Guinea. Even some of the obscure species of *Austrosimulium*, like *A. furiosum*, are now known to range from Western Australia to southern Queensland. With these extended ranges, there naturally arises the question of subspeciation. Tonnoir (MS.) had noted its occurrence in *C. fergusonii*, and we believe that we have seen it in *C. tonnoiri* and *A. torrentium*, but it has not been widely searched for, and an interesting field here awaits the investigator.

TABLE 1.

Species.	Q.	N.S.W.*	Vic.	Tas.	S.A.	W.A.	Other.
<i>Cnephia</i> —							
<i>aurantiacum</i> (Tonn.) ..		x	x	x			
<i>tonnoiri tonnoiri</i> (Drum.) ..		x				x	
<i>tonnoiri fuscoflava</i> M. and M.	x						
<i>umbratorum</i> (Tonn.) ..			x				
<i>terebrans</i> (Tonn.) ..		x	x				
sp. <i>A</i> (nr. <i>terebrans</i>) ..						x	
<i>fergusoni</i> (Tonn.) ..		x			x		
<i>fergusoni</i> var. ..						x	
<i>Simulium</i> —							
<i>ornatipes</i> Sk. ..	x	x			x	x	N.G.
<i>clathrinum</i> M. and M. ..	x						
<i>papuense</i> Wh. ..							N.G.
<i>oculatum</i> (End.) ..							N.G.
<i>wilhelmlandae</i> Smart ..							N.G.
<i>nicholsoni</i> M. and M. ..	x						
<i>faheyi</i> Tayl. ..	x						N.T.
sp. <i>B</i> (nr. <i>faheyi</i>) ..							N.T.
<i>Austrosimulium</i> —							
<i>mirabile</i> M. and M. ..	x						
<i>crassipes</i> Tonn. ..		x	x				
<i>cornutum</i> Tonn. ..		x	x	x			
sp. <i>C</i> (nr. <i>cornutum</i>) ..						x	
<i>bancrofti</i> (Tayl.) ..	x	x		x		x	
<i>pestilens</i> M. and M. ..	x						
<i>furiosum</i> (Sk.) ..	x	x	x	x	x	x	
<i>victoriae</i> (Roub.) ..	x	x	x	x			
<i>torrentium torrentium</i> Tonn.				x			
<i>torrentium hilli</i> n.subsp. ..		x					
<i>vezans</i> (Mik.) ..							N.Z.
<i>ungulatum</i> Tonn. ..							N.Z.
<i>australense</i> (Schin.) ..							N.Z.
<i>tillyardi</i> Tonn. ..							N.Z.
<i>laticorne</i> Tonn. ..							N.Z.
<i>multicorne</i> Tonn. ..							N.Z.
<i>longicorne</i> Tonn. ..							N.Z.

* Including Australian Capital Territory.

KEYS TO SPECIES.

These keys are purely for preliminary identification, and subspecies are not included. As in an earlier paper, it is considered better to rely on figures rather than keys for the identification of cocoons (Figs. 11, 20), pupae (Figs. 12, 18, 20), and larvae old enough to show a gill spot (Figs. 13D, 19).

As we have nothing to add to Tonnoir's keys (1925, pp. 230–232), the New Zealand species of *Austrosimulium* are omitted.

Females.

1. Antennae eleven-segmented 2
Antennae ten- (or nine-) segmented 14
2. Cu_1 with a gentle curve; orange to brown sps.; usually large 3
 Cu_1 with a strong double bend; dark sps.; medium-sized to small 5
3. Medium-sized brown sp., with Cu_1 almost straight, and abdomen sparsely pubescent above *C. umbratorum* (Tonn.)
Large orange sps. with Cu_1 distinctly curved, and abdomen strongly hirsute above 4
4. Propleural hairs present; wing without definite spot at fork of R .. *C. aurantiacum* (Tonn.)
No propleural hairs; wing with dark spot at fork of R *C. tonnoiri* (Drum.)
5. Abdomen with sparse, short pubescence, the general appearance of the dorsum being bare or lightly tomentose 6
Abdomen with a dense, more or less complete, covering of strong hairs and lanceolate scales 8

6. Calcipala absent or minute; propleural hairs well developed *C. fergusonii* (Tonn.)
 Calcipala well developed; propleural hairs few or absent 7
7. Small, brownish black sp.; halter with knob dark brown; lateral and apical abdominal hairs yellow *C. terebrans* (Tonn.)
 Larger, greyish black sp.; halter with knob reddish brown; lateral and apical abdominal hairs black *Cnephia* sp. *A.*
8. Prealar area bare (legs conspicuously marked with black and yellow, fore and mid coxae yellow) *S. ornatipes* Sk.
 Prealar area with a patch of pale scales (leg pattern not as above) 9
9. Scutum black, with three irregular, longitudinal golden lines; claws with strong basal tooth *S. clathrinum* M. & M.
 Scutum with pale scales more diffusely arranged; claws with at most a minute basal tooth 10
10. Minute, pale sp.; antennae entirely yellowish fawn; femora and tibiae predominantly creamy yellow *Simulium* sp. *B.*
 Small to medium spp.; antennae with only basal segments pale; femora and tibiae predominantly dark 11
11. Abdomen with last three tergites black and rather smooth *S. oculatum* (End.)*
 Abdomen with at least a scattering of pale lanceolate scales on last three visible tergites 12
12. Medium sized, stouter sp.; hind metatarsus as long as tibia *S. papuense* Wh.
 Smaller, more slender sp.; hind metatarsus shorter than tibia 13
13. Black and silvery sp.; pleurae dark grey, not contrasting with area adjacent to shoulders *S. nicholsoni* M. & M.
 More brown or grey and golden sp.; pleurae pale grey, contrasting strongly with brown markings on and adjacent to shoulders *S. faheyi* Tayl.
14. Antennae with an orange band covering fourth to sixth segments; wing with three dark spots *A. mirabile* M. & M.
 Antennae with at most the basal segments pale; wing without spots 15
15. Dorsum of abdomen with ashy tomentose markings 16
 Abdomen entirely dark dorsally 17
16. Antennae nine-segmented *A. bancrofti* (Tayl.)
 Antennae ten-segmented *A. pestilens* M. & M.
17. Claws with strong basal tooth 18
 Claws without tooth 20
18. Small, greyish sp.; abdomen with tergites covered with velvety black tomentum *Austrosimulium* sp. *C.*
 Blackish sp.; abdomen entirely dull brownish black 19
19. Larger sp.; hind metatarsus normal; calcipala nearly as wide as metatarsus, not separated by a notch *A. cornutum* Tonn.
 Smaller sp.; hind metatarsus incrassate; calcipala relatively narrower, separated by a notch *A. crassipes* Tonn.
20. Abdomen with tergites covered with velvety black tomentum *A. furiosum* (Sk.)
 Abdomen entirely dull brown, not tomentose 21
21. Larger, blackish sp. antennae long (Fig. 17A) *A. victoriae* (Roub.)
 Smaller, greyish sp.; antennae short (Fig. 17B) *A. torrentium* Tonn.
 The female of *S. wilhelmlandae* Smart (New Guinea) is not known.

Males.

1. Antennae eleven-segmented 2
 Antennae ten (or nine-) segmented 8
2. Large, orange sps. 3
 Medium to small, dark sps. 4
3. Wing without spot at bifurcation of R *C. aurantiacum* (Tonn.)
 Wings with dark spot at bifurcation of R *C. tonnoiri* (Drum.)
4. Prealar area bare; legs conspicuously marked with black and yellow *S. ornatipes* Sk.
 Prealar scales present; legs not so marked 5
5. Antennae yellow-brown; first two segments of abdomen yellow ochre *S. wilhelmlandae* Smart*
 Antennae and basal segments of abdomen dark 6
6. Upper facets of eye normally enlarged; small sp. *S. nicholsoni* M. & M.
 Upper facets of eye greatly enlarged; larger spp. 7
7. Scutum with three irregular golden lines *S. clathrinum* M. & M.
 Scutum with golden hairs diffuse *S. papuense* Wh., *S. oculatum* (End.)*
8. Antennae with orange band covering segments 4-6; wing with three black spots in radial field *A. mirabile* M. & M.
 Antennae dark (except sometimes at base); wings clear 9

* Placed here by presumption from other group characters.

9. Abdomen with shiny, lateral, ashy patches on fifth and sixth segments 10
 Abdomen entirely black 11
10. Antennae nine-segmented *A. bancrofti* (Tayl.)
 Antennae ten-segmented *A. pestilens* M. & M.
11. Hind metatarsus incrassate; calcipala small *A. crassipes* Tonn.
 Hind metatarsus normal; calcipala at least half width of shaft 12
12. Calcipala nearly as wide as metatarsus *A. cornutum* Tonn.
 Calcipala at most two-thirds as wide as metatarsus
 *A. furiosum* (Sk.), *A. victoriae* (Roub.), *A. torrentium* Tonn.

Larvae.

1. Anal sclerite without a backwardly-directed strut 2
 Anal sclerite with a backwardly-directed strut on lateral side of anterior arm 7
2. Rectal gills compound 3
 Rectal gills simple 4
3. Head pattern irregular; ventral papillae absent *S. clathrum* M. & M.
 Head pattern conspicuous, bullet-shaped; ventral papillae present *S. papuense* Wh.
4. Ventral papillae absent 5
 Ventral papillae present 6
5. Circlet with about 30 minute teeth per row *C. aurantiacum* (Tonn.)
 Circlet with 15-25 larger teeth per row *C. tonnoiri* (Drum.)
6. Head pattern positive* type; robust, dark species *S. ornatipes* Sk.
 Head pattern negative* type; more delicate, yellowish species *S. nicholsoni* M. & M.
7. Ventral papillae absent 8
 Ventral papillae present 9
8. Anal sclerite stout, angle between anterior limbs usually less than 90°; submental teeth seven *A. bancrofti* (Tayl.)
 Anal sclerite delicate, angle between anterior limbs usually greater than 90°; submental teeth eleven *A. pestilens* M. & M.
9. A chitinous rod encircling tip of abdomen ventral to anal sclerite 10
 No such rod present 12
10. Submental plate with central tooth not projecting beyond adjacent teeth; basal segment of antenna more than half length of distal segment *A. cornutum* Tonn.
 Submental plate with central tooth projecting conspicuously beyond adjacent teeth; basal segment of antenna less than half length of distal segment 11
11. Ends of chitinous ring swollen (Fig. 9) *A. mirabile* M. & M.
 Ends of chitinous ring not swollen *A. crassipes* Tonn.
12. Antennae dark brown or blackish *A. victoriae* (Roub.)
 Antennae pale 13
13. Basal segment of antenna equal in length to distal segment *A. furiosum* (Sk.)
 Basal segment of antenna markedly longer than distal segment *A. torrentium* Tonn.

The Genus CNEPHIA Enderlein.

Adults: Antennae eleven-segmented; wings with spiniform macrotrichia more or less developed on costa, but none on R₁; small cell present; pedisulcus shallow or absent. Genotype: *Simulium pecuarum* Riley, Nearctic (Sharp, 1945).

This definition is necessarily brief, details being best reserved for the groups; but we may, for the purpose of clarifying the relationships of Australian species, accept the genus *Cnephia* for those listed here, with the feeling that further study may reduce rather than increase the number of genera recognized in the *Prosimulium* complex.

The *aurantiacum* group.

Adults: Orange species, with strongly humped thorax; pubescence short, fine; palpi with terminal segment as long as the previous two together; propleural hairs present or absent; wing with Cu₁ gently sinuous; hind legs with large, conspicuous calcipala, pedisulcus shallow but distinct; claws of female with strong basal tooth; abdomen of female strongly hirsute; genital fork of *Simulium* type; male hypopygium with two spines on the style; anterior part of phallosome (Fig. 6A) with flat, very delicately setulose membrane ventrally, a strongly chitinized distal edge, and a chitinized dorsal surface; posterior part with a pair of hooks near the mid line, and patches of irregular denticles medial to distal end of apodeme; no median process detected.

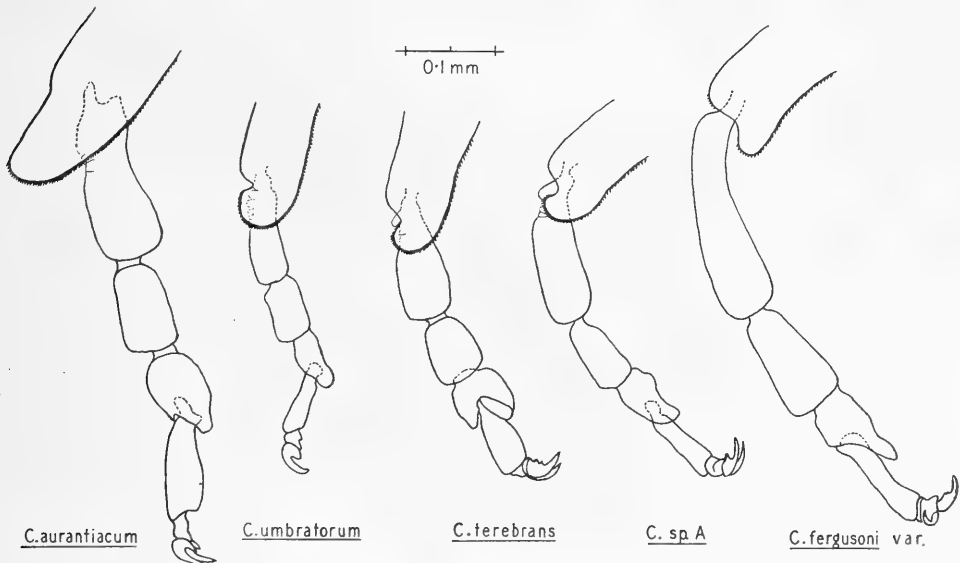
* Edwards (1934) defines the markings of the head-capsule as "positive" when the insertions of the muscles are darker than the surrounding chitin, "negative" when they are paler.

Pupa: With much branched respiratory apparatus (Fig. 11). Abdomen with a row of flat, triangular, backwardly directed, *sub-basal* spines on dorsal surface of segments 5-9; *sub-apical* dorsal and ventral hooks also present on some segments; terminal spines very large and forwardly directed (Fig. 7).

Cocoon: Coarsely woven, of indefinite shape, often incorporating foreign material (Fig. 11).

Larva: Not separable from *Simulium*, except for the pupal gill spot, the filaments of which curve first backwards and then downwards and forwards, returning upon themselves (Fig. 19, top row); anal gills simple; no ventral papillae; anterior limbs of anal sclerite without backwardly directed strut.

Smart's (1945) definition of *Cnephia* is too restrictive to fit this group, for example in describing the calcipala as "minute or absent", and he appears to be in error in saying that the pupa lacks terminal spines. On the other hand, our species show an almost perfect transition from *Cnephia* to *Gigantodax* as recognized by Edwards (1931),* and it is to be noted that the abdominal armature of the pupa is of the *Gigantodax* and not the *Cnephia* type (compare our Fig. 7 with Edwards' Fig. 12 *e* and *f*). However, *Gigantodax* has no small cell in the wing, and the respiratory organs of the pupa are rather different. *Prosimulium* itself is only to be separated by the absence of spines on costa and the forked Rs, and in both respects Australian material shows annectant forms (see Edwards', 1931, remarks on an incipient fork in Rs of *C. aurantiacum*).



Text-fig. 10.—Hind tarsi of *Cnephia* spp., females.

CNEPHIA AURANTIACUM (Tonnoir).

Simulium aurantiacum Tonnoir, 1925, p. 234. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Cnephia aurantiacum (Tonnoir), Edwards, 1931, p. 131; Smart, 1945, p. 498.

Adults: Large orange species, with yellow legs and antennae, and dark, hirsute abdomen. A group of strong, yellow propleural hairs present. Wing without dark spots at root and at fork of R, but lightly infuscated towards tip. Calcipala very large, as wide as metatarsus (Fig. 10); pedisulcus shallow but distinct. Spermatheca coarsely rugose or tuberculate.

* He incidentally shows the gently sinuous Cu_1 of *Cnephia* clearly in his Fig. 8a.

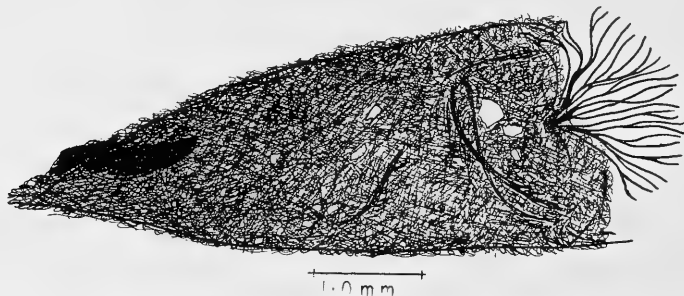
Cocoon: Coarsely woven and bag-like, but with some tendency to a simple "slipper" form; incorporates much foreign material.

Pupa: Gill-filaments relatively fine, about 40 in number.

Larva: Posterior cirlet with about 30 small teeth per row; gill-spot wide (Fig. 19).

Distribution.—Tasmania: National Park (Russell Falls), Dec.; Cradle Valley, Jan.-Feb.; St. Patrick R.; Burnie; Brunie Is.; Mt. Farrell. Victoria: Sassafras, Oct.; Mt. Dandenong (Sherbrook Falls), Oct. A.C.T.: Blundell's, Oct. New South Wales: Mt. Kosciusko (Digger's Ck.), A. J. Nicholson; Jenolan Caves, J. C. Wiburd; Brown Mt., Feb.; Fitzroy Falls, Nov.; Wentworth Falls, Nov.; Mt. Wilson, Nov. (*type locality*). All not otherwise indicated are coll. A. L. Tonnoir.

Biology: Associated with fast-running, clear mountain streams; cocoons often in moss or obscured by filamentous algae. Adults taken by sweeping vegetation along creek banks; not known to feed on blood. Tonnoir's (MS.) notes are: "This is not a common species, as it seems restricted in its habitat, which is in mountain streams—rather shady—in places where current very swift in or above waterfalls, yet where stones not bare but somewhat covered with vegetation. Also, where it occurs, it is not very abundant; the larvae are rather isolated, but pupae are found in clusters, often in moss, very rarely on stones."



Text-fig. 11.—Cocoon of *C. tonnoiri tonnoiri*, showing included foreign material.

CNEPHIA TONNOIRI TONNOIRI (Drummond).

Simulium tonnoiri Drummond, 1931, p. 6; Smart, 1945, p. 515. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Adult: Orange, with dark, hirsute abdomen; hind legs darker than in *C. aurantiacum*. No propleural hairs. Wing with a conspicuous dark mark on transverse group of veins near root, and another covering the fork of R and extending on to r-m; wing-tip clear. Calcipala and pedisulcus as in *C. aurantiacum*. Spermatheca almost smooth.

Cocoon (Fig. 11): Similar to *C. aurantiacum*.

Pupa: With 20 to 30 moderately stout gill filaments.

Larva: Posterior cirlet with 18-24 medium-sized teeth per row; gill spot (Fig. 19) distinctly narrower than in relatives.

Distribution.—Western Australia: Lesmurdie, Oct., F. H. N. Drummond (*type locality*); Perth, July, Drummond; Wongong Brook, Aug., Nicholson. A.C.T.: Canberra, Nov., Tonnoir; Coree Ck., Nov., Jan., Tonnoir.

Biology: Described by Drummond as breeding in a wide range of stream types. Habits of adults unknown.

CNEPHIA TONNOIRI FUSCOFLAVA M. and M.

Cnephia tonnoiri fusciflava Mackerras and Mackerras, 1948, p. 236. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Adult: Darker than typical subspecies; mid and hind legs suffused with black; dark rim of anterior thoracic spiracle conspicuous.

Cocoon: As in typical subspecies.

Pupa: With 15-20 gill filaments which are distinctly coarser than in typical form.

Larva: Posterior cirlet with about 15 relatively large teeth per row.

Distribution.—Queensland: Stradbroke Is., Dunwich (*type locality*), Sept. (E. N. Marks), Oct. (authors); Little Nerang R., Aug. (authors).

Biology: Early stages in small, moderately fast, clear but peaty channels in coastal strip; cocoons much obscured by filamentous algae. Habits of adults unknown.

Note.—The above three forms are closely related, and intergrade in many characters, but *C. aurantiacum* stands out by possessing propleural hairs and lacking dark spots on the wings.

The *terebrans* group.

Females: Dark, unadorned species, resembling *Austrosimulium*; thorax normal; pubescence short, fine; palpi of *Austrosimulium* type; propleural hairs present or absent; Cu_1 with a strong double curve as in *Simulium* and *Austrosimulium* (except *C. umbratorum*); calcipala present or absent; pedisulcus inconspicuous or absent; claws with large or small tooth (sometimes double) or none; abdomen with sparse, fine pubescence, giving a bare appearance as in *Austrosimulium*; genital fork of *Simulium* type, but stem relatively short.

The essential feature of this group is the combination of eleven-segmented antennae with an *Austrosimulium* abdomen. As only females are known, its affinities cannot be discussed profitably, but it clearly cannot be placed in *Simulium* (*s. str.*), and *C. umbratorum* seems to provide a link with the *aurantiacum* group. The early stages should be full of interest.

CNEPHIA UMBRATORUM (Tonnoir).

Simulium umbratorum Tonnoir, 1925, p. 237. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Cnephia umbratorum (Tonnoir), Edwards, 1931, p. 131; Smart, 1945, p. 499.

Female: Small, brown species; thorax not as strongly arched as in *C. aurantiacum*. No propleural hairs. Wing with Cu_1 almost straight (the most distinctive feature of the species—Fig. 4). Calcipala with a distinct notch at base; pedisulcus small. Abdomen brown, with pubescence on dorsum greatly reduced, though still fairly conspicuous at sides.

This species could be allotted to the *aurantiacum* group on venation, possession of a large basal tooth on the claws, and general appearance; but it has other characters which seem to relate it more closely to the *terebrans* group: terminal segment of palp but little longer than penultimate; relatively bare abdomen; relatively short stem of the genital fork, and relatively short, broad paraprocts.

Distribution.—Victoria: Fern Tree Gully, Oct., Tonnoir (*type locality*); Beaconsfield, Nov., G. F. Hill.

Biology: Known only from females collected by sweeping plants with a net.

CNEPHIA TEREBRANS (Tonnoir).

Simulium terebrans Tonnoir, 1925, p. 237. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Cnephia terebrans (Tonnoir), Edwards, 1931, p. 131; Smart, 1945, p. 499.

Female: A small brownish-black species, with dark brown legs. Terminal segment of palp only slightly longer than penultimate. No propleural hairs detected, but specimen rather rubbed. Calcipala well developed; indefinite pedisulcus, and chitin in this area weak; claws with minute tooth near base, distinct from basal projection, so that claw has a double-toothed appearance (Fig. 10). Abdomen dark brown (described by Tonnoir before dissection as having yellow hairs on apical segments and yellow lateral hair tufts).

Distribution.—Victoria: Sassafra, Oct., Tonnoir (*type locality*). New South Wales: Canoblas, Oct., E. W. Ferguson.

Biology: The type (the only specimen we have seen) was collected biting man.

CNEPHIA sp. A.

Simulium nigrum Tonnoir MS., nec *Cnephia nigrum* (Rubtzov, 1940), Sharp, 1945, p. 498. Type in School of Public Health and Tropical Medicine, Sydney.

Female: Blackish, with dark brown legs. Rather like the eastern *C. fergusonii*, but frons narrower, propleural hairs absent or reduced to a few weak ones at lower margin,

and calcipala well developed. Spinules are present on the costa. Pedisulcus present, though small. Claws with a single, well-developed, basal tooth. Abdomen black; all abdominal hairs dark, except fringe on first segment.

There is no doubt that this species is quite distinct from any other Australian member of the family.

Distribution.—Western Australia: Pemberton, Aug., Ferguson, Nicholson; Bridgetown, Aug., Nicholson.

Biology: There are no specific notes concerning this species. It was taken in company with *C. fergusonii* var., and may also have been biting man.

CNEPHIA FERGUSONI (Tonnoir).

Simulium fergusonii Tonnoir, 1925, p. 238; Sharp, 1945, p. 505. Location of type not known; paratypes in School of Public Health and Tropical Medicine, Sydney, and Division of Economic Entomology, C.S.I.R., Canberra.

Female: Large, blackish grey, very like a big *Austrosimulium*; legs uniformly brownish black. A group of well-developed propleural hairs present. Wings unusual, in that we have been unable to detect spiniform macrotrichia on the costa. No trace of calcipala nor of pedisulcus; claws without teeth, though the base is distinctly thickened. Abdomen blackish brown, resembling *Austrosimulium cornutum*.

Distribution.—New South Wales: Bumberry, Oct., Ferguson (*type locality*). South Australia: Lucindale.

Biology: The type series was taken biting man. Tonnoir (MS.) also notes: "A specimen in the collection of the School of Public Health and Tropical Medicine from Lucindale, recorded as severely injuring horses and cattle, may be one of those which were the object of Mr. Lea's note." Lea (1917) had recorded a species of *Simulium* as attacking stock in this locality in South Australia.

CNEPHIA FERGUSONI (Tonnoir) VAR.

Simulium fergusonii occidentale Tonnoir MS., nec *Simulium occidentale* Townsend, 1891, Smart, 1945, p. 510. Type in School of Public Health and Tropical Medicine, Sydney.

Female: Differs from the typical form in being distinctly more greyish in colour, with ashy reflections on thorax, and the legs a much lighter brown. The costa lacks spinules as in the typical form, propleural hairs are present, and there is no pedisulcus, but there is a distinct though minute calcipala (Fig. 10). Claws with a small tooth at base, sometimes appearing to be double.

Distribution.—Western Australia: Bridgetown, Ferguson, Nicholson; Narrogin, Nicholson; Tammin, Nicholson. All collected in August.

Biology: Some at least of the specimens were taken biting man.

The Genus SIMULIUM Latreille.

Adults: Antennae eleven-segmented; palpi variable, terminal segment sometimes as long as previous two together; thorax normal; pubescence dense, much of it in the form of lanceolate scales; propleural hairs dense and conspicuous in all species; wing with thorn-like spines among the macrotrichia on C and the greater part of R_1 ; no small cell at base; Cu_1 with a strong double curve; calcipala and pedisulcus well developed in all species; claws of female with or without tooth; abdomen of female densely covered with a mixture of hairs and scales (part of the dorsum is bare and shiny in *S. clathrinum*, but the appearance is quite unlike that of *Austrosimulium*); genital fork of female with relatively long, slender stem; male hypopygium with a single spine on style; anterior part of phallosome nearly or quite smooth ventrally (except on keel of *S. ornatipes*); posterior part differentiated, and possessing variously developed chitinizations; median process seen only in *S. ornatipes*.

Pupa: Respiratory organs with relatively few, long, rigid tubes arising from an inconspicuous base.* Abdomen with sub-basal dorsal spines confined to seventh, eighth, and sometimes ninth segments; dorsal and ventral sub-apical hooks present on some segments; terminal spine small and backwardly directed (Fig. 7).

* *S. papuense* is exceptional in having a *Cnephia* type of respiratory organ.

Cocoon: Finely woven and neatly formed; complete beneath the abdomen of the pupa.

Larva: Pupal gill spot with filaments coiled posterior to the main stem (Fig. 19); anal gills simple or compound; ventral papillae present or absent; anterior limb of anal sclerite without backwardly-directed strut. Genotype: *Rhagio colombaschensis* Fabr., Europe (Smart, 1945).

The genus is well defined in the region, and conforms adequately with Old World species. Two groups are recognized on adult characters, but the early stages are diverse and cannot be divided in the same way.

The *ornatipes* group.

Pre-alar and lower sternopleural areas bare.

One species, which is a typical *Eusimulium* belonging to Edwards' (1934) subgroup D. *S. aureohirtum* Brun. from India, Java and Sumatra appears to be closely related.

SIMULIUM ORNATIPES Skuse.

Simulium ornatipes Skuse, 1890, p. 595; Tonnoir, 1925, p. 232; Drummond, 1931, p. 6; Swan, 1937, p. 728; Taylor, 1944, p. 213; Smart, 1945, p. 510; Wharton, 1948, p. 357; Mackerras and Mackerras, 1948, p. 239. Type in Australian Museum, Sydney.

Chelocnetha biroi Enderlein, 1936, p. 117. Types in Budapest or Berlin Museum (Wharton, 1948).

Adult: Differs from all other Australian members of the genus in the group characters, in the conspicuously marked yellow and black legs, and in having yellow fore and mid coxae. *S. clathrinum* and *S. nicholsoni* occasionally (especially in recently emerged specimens) show leg markings somewhat like *S. ornatipes*, but the coxae are always dark. The male hypopygium is distinctive in having a strong ventral, spinulose median keel on the anterior part of the phallosome.

There is no doubt about the synonymy of Enderlein's species, which was pointed out by Wharton (1948). The description agrees well, and Biro collected in Sydney and New Guinea (Musgrave, 1932), from both of which localities *S. ornatipes* is known.

Cocoon: Wall-pocket type, with an irregular, mid-dorsal, anterior projection, and either no collar beneath the head (eastern specimens) or a narrow one (specimens from Western Australia).

Pupa: Head and thorax covered with small, flat tubercles. Thorax with four stout, tapering gill filaments on each side. Two forms recognized, one with short filaments (1.4 to 2 mm.) and the other with long filaments (2.5 to 3 mm.); they may occur together.

Larva: Robust, dark. Head broad, pattern on dorsum positive type (Fig. 8). Gill spot large, black, conspicuous. Anal gills simple. Ventral papillae present.

Distribution.—New Guinea: Moresby district, June, D. J. Lee and R. H. Wharton. Queensland: Rockhampton district; Dawson and Burnett R. watersheds; Brisbane R.; Brisbane; South Coast district; Stanthorpe district; Condamine R. and tributaries; Cunnamulla. Found at various times of year except early summer. New South Wales: Many coastal and tableland streams between Queensland border and Newcastle, Mar. and Aug., D. Mackerras; Gosford, May, D. Mackerras; Oxford Falls, Wharton; Sydney, June, F. A. A. Skuse, Sept., F. H. Taylor, Sep.-Dec., Ferguson; Hartley (Lett R.), Dec.-Jan., Wharton; Bathurst (Fish R.), Apr., Wharton; Glanmire (3,000 ft.), Apr., Wharton; Darling R., Louth (*type locality*), Helms; Bourke; Wilcannia. A.C.T.: Canberra, Molonglo R., Oct.-May, Cotter R., Dec.-Apr., Tonnoir. South Australia: Waterfall Gully, Jan.; Wakefield R., Jan.; Glen Osmond, May; all coll. D. C. Swan. Western Australia: Darling Range area, presumably spring and early summer, Drummond; Dalgarpur Brook, Aug., Nicholson. Not recorded from Victoria or Tasmania.

Biology: We have already discussed the biology of this species in some detail (Mackerras and Mackerras, 1948). It is the most widespread and usually the most abundant Simuliid in Australia, but the adults have rarely been seen in nature, and are not known to take blood. Early stages abound in almost every moderate to sluggish, fairly clear stream or channel in which water runs for more than a few weeks, and

have even been found in still rock-pools, into which they were probably washed by a recent freshet (Wharton, personal communication). They prefer submerged grass-blades and other vegetation, but also occur on stones. The duration of the life-cycle in warm weather is probably about three weeks.

Tonnoir had two interesting notes on this species at Canberra.

1. He collected large numbers of males "dancing in swarms at sunset at highest point of Deakin Park, 20 Mar., 1935". This point is more than $1\frac{1}{2}$ miles from the river.

2. "At the end of May, 1931, some larvae were observed in the aquarium with rather small, not always easily detectable *Mermis* worms. These larvae were isolated in breeding cascade and died within a week, the worm increasing to a very large size and turning a dark colour within the last few days. The worm bores a hole in the side of the larva to get out; the larva collapses completely and dies. The histoblasts did not develop, as mentioned by Strickland. Two worms were placed in damp soil in a crystal dish, but, when examined a week afterwards, no trace of them was found."

The *clathrinum* group.

Membranous prealar area bearing numerous lanceolate scales; lower sternopleural area with evenly spaced, short, erect hairs. Legs usually with greater part of hind metatarsus pale.

This group appears to be near Edwards' (1934) sub-group C, for he describes the lower sternopleural hairs and the rather characteristic leg markings, though he does not mention the prealar scales. These are so conspicuous (at any rate in fresh specimens) that we doubt whether they could have been present in the Oriental species.* This character appears to have been used previously only by Gibbins (1934), followed by de Meillon, for the *hirsutum* group in the Ethiopian fauna. His figures, however, indicate a rather different appearance and arrangement of the hairs, and we do not suggest that the *hirsutum* and *clathrinum* groups are faunistically related.

Owing to the close relationship of the adults, longer descriptive notes are necessary than elsewhere in this paper.

SIMULIUM CLATHRINUM M. and M.

Simulium clathrinum Mackerras and Mackerras, 1948, p. 248. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: Medium sized, rather thick-set, very dark species. Frons one-seventh head width. Scutum black, with three somewhat indefinite golden lines on disc and creamy reflection at sides. Wings with veins at base black and included membrane infuscated. Legs with conspicuous silvery or creamy scales on femora and tibiae, as well as on pale part of hind metatarsus. Claws with a distinct basal tooth. Abdomen with usual silvery fringe to first segment; second to fourth covered with black scales; remainder shining black dorsally.

Male: Upper facets of eyes unusually enlarged, about the size of second antennal segment. Thorax with golden lines as in female. Wings and legs similar to female, but pale scales on femora and tibiae more golden and less conspicuous. Abdomen black, except for sublateral, ashy, shining patches on second, fifth and sixth segments. Hypopygium with anterior part of phallosome without keel and not transversely ridged below, bare on centre, but with some short hairs and spinules laterally.

Cocoon: Characteristic; sub-conical, with a distinct anterior collar, which is prolonged all round into a latticed portion surrounding the gill filaments of the pupa (Fig. 20).

Pupa: With four long, slender, pointed, dark gill filaments arising from a short, dark stem on each side.

* Mr. Paul Freeman has informed us that there are no prealar scales or hairs on any of Edwards' species from Java and Sumatra in the British Museum.

Larva: Robust, dark. Head with a ventral incisure, pattern positive type, irregular in shape. Gill-spot rather small, pear-shaped. Rectal gills compound. Ventral papillae absent, but ventro-lateral swellings present.

Distribution.—Queensland: South Coast district (Lower Mudgeeraba Ck. *type locality*), March, May, June; Brisbane, June; Brisbane R., May; Samford district, April; Gayndah, May; Eidsvoid, May.*

Biology: Early stages on stones, grass blades and sometimes logs in swiftly running, clear water, most numerous where flow most powerful; pupae sometimes in dense masses. Habits in adults unknown.

SIMULIUM PAPUENSE Wharton.

Simulium papuensis Wharton, 1948, p. 359. Type in Macleay Museum, University of Sydney.

Female: Close to *S. clathrinum*, but differs in that the golden scales on the scutum are not concentrated into three longitudinal lines, veins at the root of the wing are paler (brown), and the teeth on the claws, if present, are much smaller. Abdomen with all segments clothed with scales dorsally; first with a creamy gold fringe; second quite densely covered with creamy gold scales; third dark, with a rather scattered apical line of pale scales; fourth with the pale scales more numerous on disc, but still predominantly apical; fifth and sixth with the pale scales fairly evenly diffused over disc; apical segments hidden in the specimens we have seen.

Male: The upper eye-facets are even more enlarged than in *S. clathrinum* (Wharton, 1948, fig. 8); otherwise the male is only to be distinguished by the uniform distribution of the golden scales on the scutum. Hypopygium with the anterior part of the phallosome more like that of *S. nicholsoni*, broad, appearing transversely ridged, and very delicately spinulose below.

Cocoon: Sub-cylindrical, rounded posteriorly, rather delicate, with a fenestrated collar beneath head anteriorly, and with the lateral margins swept back to expose the greater part of the thorax of the pupa.

Pupa: Gill filaments remarkable, strongly arborescent, like those of the species of *Cnephia* described above. The abdominal chaetotaxy is, however, normal and the terminal spines are quite small.

Larva: Robust; close to *S. clathrinum*, and is the only other known Australasian species with compound anal gills. Distinguished by the broad, conspicuous, bullet-shaped, median dark stripe on the head (Fig. 8), extremely deep ventral incision of the head capsule (almost reaching the submentum), presence of ventral papillae, and the large gill-spot, which is not as dark as that of *S. ornatipes*. The filaments are coiled in normal *Simulium* fashion (cf. *Cnephia*).

Distribution.—New Guinea: Pt. Moresby, June, Lee and Wharton (*type locality*); Milne Bay, Mackerras.

Biology: Early stages on stones in small creek with a moderate flow. Habits of adults unknown.

SIMULIUM OCULATUM (Enderlein).

Pselaphochir oculata Enderlein, 1936, p. 121. Types presumably in Budapest or Berlin Museum (Wharton, 1948).

Simulium oculata (Enderlein) Smart, 1945, p. 510; Wharton, 1948, p. 358.

We have not seen this species, but it appears to belong here. The male has greatly enlarged upper eye facets, like *S. papuense*. The female is separable from *S. clathrinum* by the uniformly distributed golden hairs on the scutum and the untoothed claws, and from *S. papuense* by the rather smooth, black (apparently bare) last three abdominal tergites. Enderlein does not mention any pale zone on the hind metatarsus, which may be a distinguishing character in both sexes.

Distribution.—New Guinea: Sattleburg (Huon Gulf), Nov., Biro (*type locality*).

* Mr. Wharton has discovered a closely related species in the Blue Mts. and Sydney District, N.S.W.

SIMULIUM WILHELMLANDAE Smart.

Wilhemia pygmaea Enderlein, 1922, p. 70 (*nec Simulia pygmaea* Zetterstedt, 1838). Type possibly in Budapest or Berlin Museum (Wharton, 1948).

Morops pygmaeus Enderlein, 1930, p. 93; Edwards, 1934, p. 118.

Simulium wilhelmlandae Smart, 1944, p. 131 (*nom. nov.*); Wharton, 1948, p. 358.

Male: We have not seen this species, but it almost certainly belongs here, for it has the upper facets of the eye greatly enlarged, mesosternal hairs, and the characteristic colouration of the hind metatarsus (Edwards, 1934). It should be easy to recognize by its bright brown-yellow antennae and yellow-ochre first two segments of the abdomen.

Distribution.—New Guinea: Kaiser Wilhelmland (= Mandated Territory of New Guinea), Hollsong (*type locality*).

SIMULIUM NICHOLSONI M. & M.

Simulium nicholsoni Mackerras and Mackerras, 1948, p. 251. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: A rather small, dark species, more slender than *S. clathrinum*, and with frons one-fourth head width. Antennae with first two segments and base of third brownish yellow, remainder deep brown. Scutum with numerous pale scales, which are golden towards the centre, more silvery at the sides, and with dark, converging dorso-central lines; shoulders almost black; pleurae dark man-o'-war grey, with but faint indications of ashy reflections, the only brown part being the membranous prealar area; prealar scales silvery. Wings with veins at root yellowish to brown. Legs with silvery scales on femora and tibiae, hind metatarsi largely pale; claws humped at base but not toothed. Abdomen covered with brownish black scales; fringe of first segment with silvery reflections; second with an apical, transverse silvery band; third and fourth dark medially, with silvery apical patches laterally; subsequent segments with sprinkling of pale scales on disc as well as the lateral silvery zones.

The general appearance of this species is silvery and black.

Male: A black species, with ashy lateral patches on the abdomen. Bears a superficial resemblance to the males of *A. bancrofti* and *A. pestilens*, from which it is to be distinguished by the generic and group characters. It is to be separated from *S. clathrinum* by lacking the golden thoracic lines, and on rubbed specimens by the hypopygium, the anterior part of the phallosome being relatively broader, with distal edge curled backwards (giving the appearance of a transverse ridge) and very delicately spinulose ventrally.

Cocoon: A simple, finely woven wall-pocket, without anterior collar or dorsal projection.

Pupa: With six, rather narrow, straight gill-filaments arising from a slender stem on each side, directed forward and lying close together in a characteristic fashion.

Larva: Rather delicate, characteristically yellowish in colour. Head pattern of negative type (Fig. 8). Gill spot small, pear-shaped. Anal gills simple; ventral papillae present.

Distribution: Queensland: Many localities from the South Coast and Brisbane districts to the Mackenzie R. (Fitzroy watershed) and westward to Dalby (Condamine watershed). The *type locality* is Brisbane R. (Wivenhoe). Collected from April to June and again in January. New South Wales: Bathurst (Fish R.), Apr., Wharton.

Biology: Common and widespread, but the adults have rarely been seen, most being collected by sweeping *Metaleuca* in creek beds, and an occasional specimen while making half-hearted attempts to bite man (E. N. Marks). Early stages in moderately fast, fairly clear to somewhat muddy water, usually attached to submerged vegetation, dead sticks, and leaves or logs. Its place in the succession of species which follow flooding is between *A. bancrofti* and *S. ornatipes* (Mackerras and Mackerras, 1948). It must have a resistant stage to carry it through periods of drought.

SIMULIUM FAHEYI Taylor.

Simulium faheyi Taylor, 1927, p. 71; Sharp, 1945, p. 504; Mackerras and Mackerras, 1948, p. 255. Type (labelled "Allotype") in School of Public Health and Tropical Medicine, Sydney.

Female: Close to *S. nicholsoni*, but the general colouration is brown or grey and golden rather than black and silvery. In particular, the prealar scales are creamy to golden, the legs are brown with pale golden scales, and the dark scales on the dorsum of the abdomen are a rich brown in colour. The shoulders are brown, the colour extending down on to the pleura in a patch behind the pronotal lobes and posteriorly in a narrow zone around the anterior spiracle to join the brown prealar area. The remainder of the pleural surface is pale grey with distinct ashy reflections, so that there is a contrast in colours which is not seen in *S. nicholsoni*. The claws were described by Taylor as toothed; the basal thickening is pointed in the type (forming an indication of a tooth) but not in the other specimens we have seen.

Distribution.—Queensland: Innisfail, Taylor (*type locality*); Lawn Hill (near Burketown), May, Mackerras. Northern Territory: Brocks Ck., Apr., T. G. Campbell; Adelaide R., March, A. R. Woodhill.

Biology: The type was taken by sweeping vegetation along a creek. Campbell notes his specimens as giving a severe bite.

SIMULIUM sp. B.

Female: A single specimen of the *clathrinum* group from the Northern Territory is new to the region. It is very small (body 1.3 mm.). Frons one-third of head width; antennae light fawn throughout. Thorax grey, with silvery scales. Wing with light cream veins and hairs, but black spinules on C and R₁; R appears to be bare (a unique character in the region), but the pale hairs of this species are exceedingly difficult to detect without mounting a wing. Legs with the greater part of mid and hind femora and tibiae and of hind metatarsus pale yellow; claws without teeth. Abdomen with basal four segments brown dorsally, covered with brown and some golden scales; remainder grey, tomentose, with rather scattered creamy scales.

This species should be easy to recognize, when material adequate for naming it is discovered. Its nearest relative may be *S. wilhelmlandae* from New Guinea.

Distribution: Northern Territory: Adelaide R., Mar., Woodhill.

The Genus AUSTROSIMULIUM Tonnoir.

Adults: Small to medium, dark or greyish species; antennae ten- (occasionally nine-) segmented; palpi with terminal segment about two-thirds as long as previous two together; thorax normal; pubescence short, fine; propleural hairs present or absent, never conspicuous; wings with spines among the macrotrichia on costa, but none on R₁; small cell present, though often poorly defined; Cu₁ with a strong double curve; calcipala and pedisulcus well developed in all species; claws of female usually simple, sometimes with a strong tooth at base; abdominal pubescence of female short and scanty, so that the dorsum appears either bare but rather dull, or covered with delicate, velvety tomentum; genital fork of female with stem relatively short and broad; male hypopygium with three (occasionally four or two) spines on style; ventral surface of anterior part of phallosome strongly swollen and setulose; posterior part membranous, often swollen, armed with groups of delicate, pale denticles; median piece sometimes lightly chitinized, usually impossible to detect.

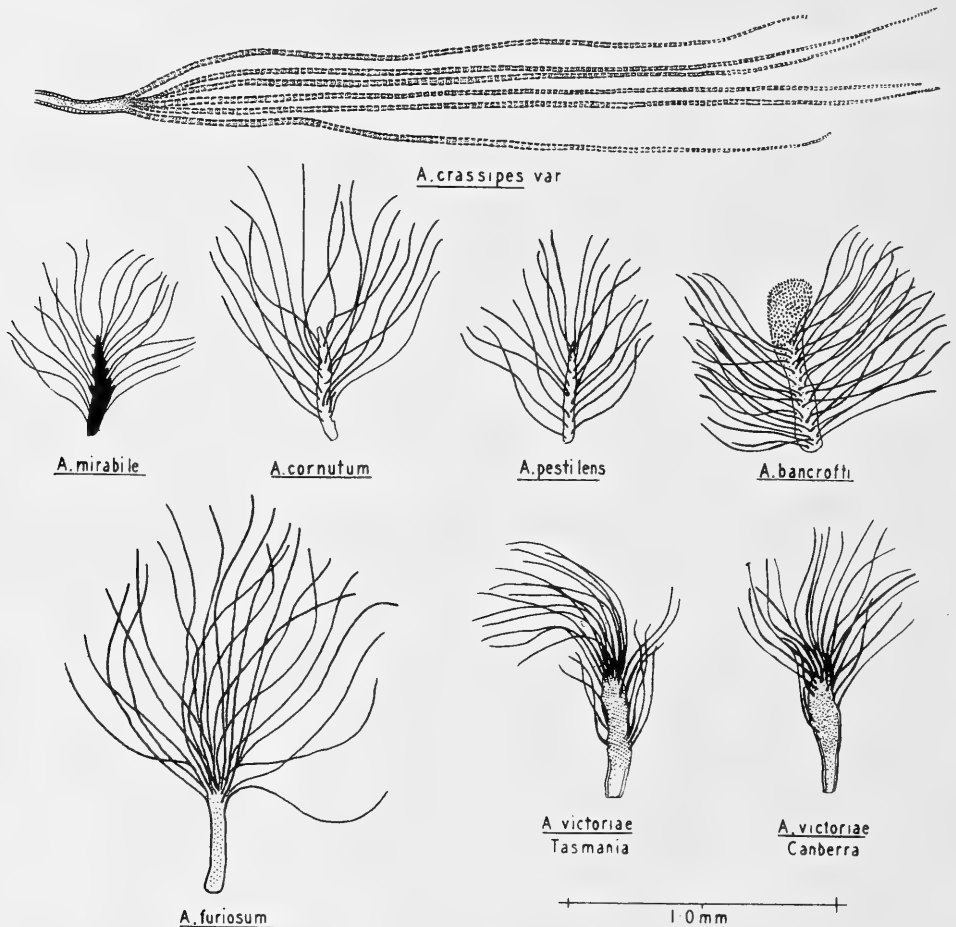
Pupa: Respiratory organ (Fig. 12) usually characteristic, a clavate, tapering, or spatulate horn bearing numerous fine, unbranched filaments,* which appear as if composed of a large number of short, delicate segments. Abdomen with no sub-basal dorsal spines on any segment; sub-apical dorsal hooks present on a variable number of segments; sub-apical ventral hooks usually absent; terminal spines small, backwardly or inwardly directed (Fig. 7).

Cocoon: Finely woven and neatly formed; deficient ventrally in its hinder part, so that the abdomen of the pupa lies on the substrate.

* *A. crassipes* (Fig. 12) and two New Zealand species have a relatively short stem and fewer, longer, wider filaments.

Larva: Pupal gill-spot with filaments curving anteriorly and upwards from the main stem; anal gills simple; ventral papillae present or absent; anterior limbs of anal sclerite each with a slender, backwardly-directed strut (Figs. 9, 18)—this feature immediately distinguishes *Austrosimulium* larvae from those of any other genus in the region, though it is figured by Gibbins (1934) in two Ethiopian species of *Simulium*; in some species an incomplete chitinous strut encircles the tip of the abdomen ventral to the posterior limb of the anal sclerite.*

Genotype: *Simulium australense* Schiner, from Auckland, New Zealand, by original designation (Tonnoir, 1925, p. 230).



Text-fig. 12.—Pupal respiratory horns of Australian species of *Austrosimulium*.
(For *A. torrentium* see Fig. 18.)

Austrosimulium is the best differentiated genus in the region, and is easily recognizable at all stages. In lacking spines on R_1 and possessing a small cell, it would appear to lie closer to the *Prosimulium* complex than to *Simulium*. The *terebrans* group is a possible link in *Cnephia*. Also, Puri (1926) has described the pupal breathing horn

* An almost complete ring is formed by the posterior limbs and this strut, and it lies immediately anterior to the posterior circlet of hooks. Its position was mistaken by Sharp (1945, footnote to p. 486), who apparently thought that the ring was formed in relation to the anterior limbs of the anal sclerite.

of *Prosimulium ferrugineum* as resembling the *Austrosimulium* type, while Edwards (1931) has pointed out that the ventral arms of the anal sclerite of the larva surround the tip of the abdomen only in *Gigantodax* and some species of *Austrosimulium*.

AUSTRALIAN SPECIES.

Three groups are recognized on female and larval characters. Pupae are diverse.

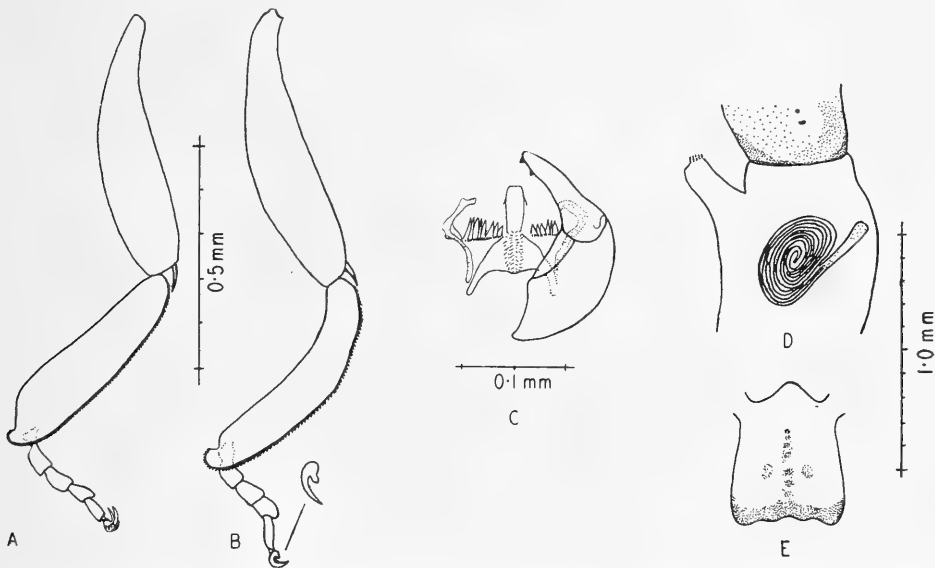
The *mirabile* group.

Claws of female strongly toothed; abdomen various. Larva with incomplete, dark, chitinous ring surrounding tip of abdomen anterior to circlet; ventral papillae present. Shows relationship with New Zealand species.

AUSTROSIMULIUM MIRABILE M. & M.

Austrosimulium mirabile Mackerras and Mackerras, 1948, p. 266. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Adult: Both sexes are easily recognized by the very long, dark antennae, with an orange band covering segments four to six, and by the presence of three dark spots in the radial field of the wing. Dorsum of abdomen with ashy, tomentose markings in both sexes, supplemented by patches of brilliant white scales in female. Style of male hypopygium with only two teeth.



Text-fig. 13.—A. *crassipes* var. A. Leg of male. B. Leg of female, with enlarged claw to show tooth characteristic of group. C. Hypopygium of male. D. Gill-spot of larva. E. Head pattern of larva.

Cocoon: Wall-pocket type, often flattened at sides and almost circular in dorsal view; without collar, and with a small, mid-dorsal, anterior projection.

Pupa: Respiratory horn black, pointed, covered with longitudinal spiny ridges. Numerous filaments, about as long as the horn, arise from the furrows between the ridges.

Larva: Distinguished from relatives only by the characters given in the key, and the gill-spot which is elongate-oval and conspicuous by reason of the jet-black respiratory horn.

Distribution.—Queensland: Dawson Ck. on slopes of Mt. Glorious, Apr. (*type locality*).

Biology: Early stages on dead leaves in moderately fast, clear water. Habits of adults unknown.

AUSTROSIMULIUM CRASSIPES Tonnoir.

Austrosimulium crassipes Tonnoir, 1925, p. 242; Smart, 1945, p. 499. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Mr. R. H. Wharton has recently collected the early stages and bred out adults in the Blue Mountains, New South Wales. His males conform well to the hitherto unique type, including the details of the hypopygium, and differ only in that the hind metatarsus is not so incrassate. We feel that these specimens should be regarded at most as a geographical race of *A. crassipes*, but an element of doubt must remain until the early stages are discovered in Victoria. The notes below are based mainly on Mr. Wharton's material.

Female: A dark species, with unusually long creamy-yellow hairs on scutum and legs, and entirely dull, brownish black abdomen. Generally like a small *A. cornutum*, but the hind metatarsus is wider and the calcipala differently shaped (cf. Figs. 13B and 15).

Male: Immediately distinguished by the incrassate hind metatarsus (Fig. 13A, cf. also Tonnoir, 1925, Fig. 2, I). The style of the hypopygium has only two teeth; the setulose area on the anterior part of the phallosome is more restricted than usual; the posterior part bears a row of long, though delicate, teeth on each side; and the large median piece can be distinctly seen (Fig. 13C).

Cocoon: Similar to *A. mirabile*, but with a narrow collar, and sometimes a larger dorsal projection (Fig. 20).

Pupa: Distinguished by the six remarkably long gill filaments arising from a short stem, the whole respiratory organ being as long as the cocoon. Superficially a relationship to *S. nicholsoni* might be suggested, but the segmented appearance of the filaments (Fig. 12) is an *Austrosimulium*, not a *Simulium* character.

Larva: Younger larvae resemble *A. mirabile* closely, but the dorsal ends of the chitinous ring are not expanded (cf. Fig. 9), and the number of teeth per row in the circlet is 15-20 as compared with 12-15. Gill-spot unique in the genus by reason of the evenly coiled filaments (Fig. 13D).

Distribution.—Victoria: Sassafra, Oct., Tonnoir (*type locality*). New South Wales: Mt. Victoria, December-March, Wharton; Wentworth Falls, Mar., Wharton.

Biology: Tonnoir's specimen was collected by sweeping vegetation along a creek. Mr. Wharton's larvae were found on leaves and the pupae on stones in small mountain streams.

AUSTROSIMULIUM CORNUTUM Tonnoir.

Austrosimulium cornutum Tonnoir, 1925, p. 243; Smart, 1945, p. 499. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: A relatively large, dark species, like *A. victoriae*, but immediately distinguished by the strongly toothed claws. Frons about one-quarter head width; antennae long (as in *A. victoriae*, Fig. 17A); legs rather uniformly brown; calcipala nearly as wide as metatarsus; abdominal tergites dull brown, without trace of black tomentum.

Male: Recognizable from other dark species only by the wide calcipala. There are two teeth on the style of the hypopygium, as in *A. crassipes*.

Cocoon: Oval, apparently without collar, but with a single, long, median, dorsal projection "curving downwards so as to protect the head of the nymph" (Tonnoir).

Pupa: Respiratory horn strong, brown, tapering, with numerous filaments arising all over surface. It is rather like that of *A. mirabile*, but the horn is not black and not so ridged.

Larva: Distinguished from its relatives only by the characters listed in the key, and by the S-shaped gill-spot rather like that of *A. furiosum* (Tonnoir, 1925). The basal segment of the antenna, though longer than in *A. mirabile*, is still markedly shorter than the distal segment (Fig. 16).

Distribution.—Tasmania: Burnie, Oct.; St. Patrick R., Nov.; National Park, Dec.; King R., Feb.; Strahan, Feb.; Mt. Wellington; Cradle Mt.; Eagle-Hawk Neck, Nov.; Maria Is., Nov.

Victoria: Sassafras, Oct. (*type locality*). New South Wales: Mt. Kosciusko (Sawpit Ck., Pretty Pt. Ck.), Dec.; Fitzroy Falls, Nov.; Wentworth Falls, Nov. A.C.T.: Coree Ck., Sept., L. Graham. All but the last coll. Tonnoir.

Biology: Adults collected by sweeping, not observed to bite. Early stages in very swift water, rather scattered, never in colonies (Tonnoir).

AUSTROSIMULIUM sp. C.

Female: Only a single specimen known. Related to *A. cornutum*, having the same type of claws with a powerful tooth at base, but differs in its smaller size, narrower frons (one-eighth of head width), fawn-coloured legs, and in having velvety black abdominal tergites 2-6, which are like those of *A. furiosum* but smaller. A well differentiated species, but we lack the material to describe it adequately.

Distribution.—Western Australia: Pemberton, Aug., Nicholson.

The *bancrofti* group.

Claws of female simple; abdomen with ashy central patches, forming a median dorsal stripe. Larva without chitinous ring; ventral papillae absent.

AUSTROSIMULIUM BANCROFTI (Taylor).

Simulium bancrofti Taylor, 1918, p. 168; Taylor, 1927, p. 70 (part). Type female (labelled "Allotype") in School of Public Health and Tropical Medicine, Sydney.

Austrosimulium bancrofti (Taylor), Tonnoir, 1925, p. 241 (part); Drummond, 1931, p. 8; Smart, 1945, p. 499; Mackerras and Mackerras, 1948, p. 256. An allotype male, from Serpentine, Western Australia, was labelled by Drummond, and placed in Division of Economic Entomology, C.S.I.R., Canberra.

Female: A medium to small, greyish species. Antennae nine-segmented, third segment enlarged (Fig. 1); first two segments creamy yellow. Abdomen with a wide, discontinuous, ashy dorsal stripe, distinguishing this species from all others except *A. pestilens*. Legs with considerable pale fulvous suffusion.

Male: Black. Antennae nine-segmented. Abdomen with a conspicuous patch of ashy tomentum laterally on fifth and sixth segments. Hypopygium with style distinctly longer than coxite.

Cocoon: Shoe-shaped, with a conspicuous anterior collar, which is deeper than in any other species. The opening is well swept back, and there is no mid-dorsal projection.

Pupa: Respiratory horn flat, spatulate. The filaments are about as long as the horn, and arise from the whole of the outer surface except the distal fourth, which is spinulose.

Larva: Head usually fairly heavily pigmented; submental teeth seven. Gill-spot elongate, club-shaped (very characteristic). Anal armature with anterior limbs forming less than a right-angle. Posterior circler with 20-30 spines per row.

Distribution.—Queensland: Mackenzie, Dawson and Burnett R. basins (*Eidsvold type locality*); Brisbane R.; Brisbane; South Coast; Dalby; Chinchilla; Goondiwindi, J. L. Wassell; Roma, R. A. J. Meyers. Collected between March and August. New South Wales: Hartley (Lett R.), Dec., Wharton; Bathurst (Fish R.), Apr., Wharton; Bumbery, Oct., Ferguson*; Bourke, May, Ferguson*; Yass, Aug., Nov., K. English. A.C.T.: Molonglo R., Sept.-Apr., Tonnoir; Black Mt., June, Hill, Nov., F. J. Gay; Cotter R., Nov.-Apr.; Murrumbidgee R., Jan.; Blundell's, Sept., Dec., Feb., Tonnoir; Lee's Spring, Oct., Hill; Brindabella, Oct., L. Willings. Tasmania: Launceston, Apr., M. Crust. Western Australia: Darling Range area, spring and early summer, Drummond; Serpentine, Apr., Drummond; Mundaring, Aug., Ferguson; Bridgetown, Aug., Nicholson. Not yet known from Victoria or South Australia.

Biology: Been taken biting man, more frequently in the southern and western parts of its range than in Queensland. Early stages in very fast-moving, fairly clear to definitely muddy water; usually attached to submerged *Melaleuca* fronds, sticks, logs, dead leaves, and occasionally stones. Larvae crowd together in dense masses. Comes next after *A. pestilens* in the succession which follows flooding of inland streams. Must possess a drought-resistant stage.

* Identification not confirmed; could have been *A. pestilens*.

AUSTROSIMULIUM PESTILENS M. & M.

Simulium bancrofti Taylor, 1927, p. 70 (part).

Austrosimulium bancrofti (Taylor), Tonnoir, 1925, p. 241 (part).

Austrosimulium pestilens Mackerras and Mackerras, 1948, p. 260. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: Very close to *A. bancrofti*, from which it is to be distinguished primarily by the ten-segmented antennae. Also, it is usually smaller, the head is distinctly narrower, the basal segments of the antennae are darker, the third segment is smaller, and the legs are more uniformly brown.

Male: Only separable from *A. bancrofti* by the ten-segmented antennae and the style of the hypopygium not being quite as long as the coxite.

Cocoon: Collar not as high as in *A. bancrofti*, often quite low, but the shape is variable owing to the general crowding together of the cocoons.

Pupa: Respiratory horn slender, pointed (cf. the spatulate horn of *A. bancrofti*), with irregular surface, from the whole of which the slender filaments arise; they are a little longer than the horn. *A. cornutum* and *A. mirabile* have similar respiratory organs, but the horn of the latter is dark, and both have ventral spines on the abdomen, whereas there are only ventral hairs in *A. pestilens*.

Larva: Head very pale, with only a trace of median marking. Submental teeth eleven. Gill-spot small, oval. Anal armature with anterior limbs diverging at more than a right-angle. Posterior circlet with 10-12 spines per row.

Distribution.—Queensland: Widespread from Wowan in Central Queensland to the New South Wales border near Dirranbandi, and inland to Windorah. Not known from east of the Divide, except on the Dawson and Upper Burnett Rivers. Collected from January to April. (Chinchilla *type locality*). New South Wales: Not recorded, but almost certainly present in north-western districts.

Biology: This species is the pest Simuliid of Queensland, and its behaviour has already been discussed (Mackerras and Mackerras, 1948). The adults swarm after floods and attack kangaroos, domestic animals and man. The early stages are only found in very fast, turbulent, muddy water. There is an association with *Melaleuca* spp.; the early stages crowd on the submerged parts and cocoon in dense masses on the fronds, while the adults rest in thousands on the exposed parts of the trees. It is first in the succession of species which follows flooding, and evidently has a drought-resistant stage to tide over the periods when the streams are sluggish or dry.

The *furiosum* group.

Claws of female simple; abdomen entirely dark. Larva without chitinous ring; ventral papillae present.

This is a group of species, which Tonnoir considered easy to recognize in the pupal stage, but difficult to separate as adults. We have been unable to distinguish satisfactorily between the males, but the females are better differentiated, and the three types recognized (and these only) could be correlated with well-defined pupal characters. In brief: *furiosum* has the abdominal tergites velvety black; *victoriae* is longer, darker, with relatively long antennae (Fig. 17A; *A. furiosum* is similar); *torrentium* is more compact, greyish, and with distinctly shorter antennae (Fig. 17B; the relative length is similar in *A. bancrofti* and *A. pestilens*). The basic characteristics of the pupae are constant in the three species, but they show some variation in such features as the lengths of the horn and filaments. We are unable to accept these relative differences as justifying specific or subspecific recognition, unless they are accompanied by differences in other stages also.

AUSTROSIMULIUM FURIOSUM (Skuse).

Simulium furiosum Skuse, 1888, p. 1362. Type in Macleay Museum, University of Sydney.

Austrosimulium furiosum (Skuse), Tonnoir, 1925, p. 239; Smart, 1945, p. 499; Mackerras and Mackerras, 1948, p. 264. Allotype male, morphotype larva and pupa, from Gosford, March, D. Mackerras, in Division of Economic Entomology, C.S.I.R., Canberra.

Austrosimulium simile Tonnoir, 1925, p. 249. Type in Division of Economic Entomology, C.S.I.R., Canberra.

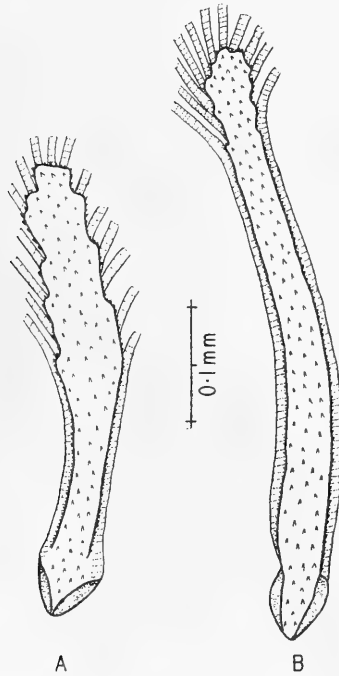
Austrosimulium austrosimile Smart, 1944, p. 133.

Austrosimulium weindorferi Tonnoir, 1925, p. 248. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: A medium-sized, dark species; frons about one-fourth head width; antennae long (Fig. 1); propleural hairs present or absent; legs brown, often with darkened tips to femora, tibiae and metatarsi; calcipala from half to two-thirds width of metatarsus; abdomen dark brown or greyish, tergites 2 to 6 velvety black, showing up as conspicuous black patches against the dull ground colour; the posterior edges of the tergites are sometimes narrowly banded with ashy tomentum.

Male: Rather small, black, undistinguished. Scutum velvety black, with dark golden hairs; abdomen velvety black; legs darker than in female. Calcipala about two-thirds the width of the metatarsus, and third antennal segment nearly twice as long as the fourth. Style of hypopygium with three teeth; posterior part of phallosome with a row of denticles on each side of distal margin.

Cocoon: Simple wall-pocket, with the sides just meeting in front, and no central dorsal projection.



Text-fig. 14.—Pupal horns of *A. furiosum*, showing range of variation.

Pupa: The respiratory horn is a slender, rather pale, finely spinulose cylinder, ending distally in an irregularly conical prolongation, from which 20 to 30 slender filaments arise. The filaments are banded with exceedingly minute spines, giving them rather the appearance of striated muscle fibres. Usually the horn is about six times as long as wide (Figs. 12, 14B) and the filaments about twice as long as the horn, but both may be shorter.

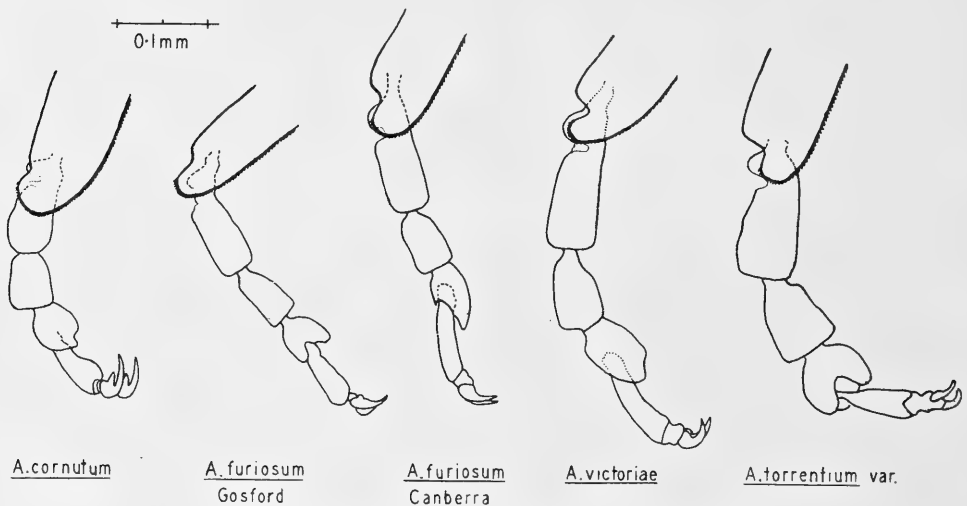
Larva: Antennae pale, distal segment* about as long as basal. Head with an irregular central pattern, and a sublateral dark spot on each side (a useful character for

* Actually the antennae of Simuliid larvae appear to be four-segmented, the stouter first and second being more or less fused together, the third long and slender, and the fourth very short. We have followed custom and convenience in amalgamating the first and second pairs.

preliminary, low-power diagnosis). Gill-spot S-shaped (cf. *A. cornutum*). Anal sclerite delicate.

Synonymy: Our identification of *A. furiosum* is based on fresh material (larvae, pupae, bred adults) collected at Gosford by D. Mackerras, the females being compared with Skuse's type material by Mr. R. H. Wharton. There is no doubt of the identity of Tonnoir's *A. simile* with this species. Smart's *austrosimile* was a *nom. nov.*, as *simile* was preoccupied in *Simulium*. *A. weindorferi* Tonn. differs only in the shorter pupal respiratory horn and filaments (Fig. 14A). Structurally, however, both horn and filaments are exactly the same in the two, as are the larvae and adults. We have seen a few "short-horned" *A. furiosum* from Queensland (cf. also *S. ornatipes*), and feel that *A. weindorferi* is only a variant which does not merit subspecific status.

Distribution.—Queensland: Noosa, Aug., Marks; Nerang, Mar., authors; Mudgeeraba Ck., May, authors; Logan R., June, Marks; Dalby, Apr., authors. New South Wales: Armidale, Aug., D. Mackerras; Carlisle's Gully (N. of Tamworth), Aug., D. Mackerras; Gosford (*type locality*), Aug.-Sept., Skuse, Mar. and May, D. Mackerras; Berowra, Aug.-Sept., Skuse; Hartley (Lett. R.), Dec., Wharton; Bathurst (Fish R.), Apr., Wharton; Oberon (Fish R., 4,000 ft), Apr., Wharton; Wentworth Falls, Mar., Wharton; Tallong, Sept., Taylor; Deniliquin, Nov., Ferguson. A.C.T.: Molonglo R., Sept.-Nov.; Black Mt., Oct., Cotter R., Oct.-Dec.; Cotter-Murrumbidgee Junction, Oct.; Murrumbidgee R., Jan.; Blundell's, Jan., Feb., Apr., Graham; Lee's Spring, Nov., Hill; all but last two coll. Tonnoir. Victoria: Morrison's; Cockatoo, Oct.; Fern Tree Gully, Dec.; Beaconsfield, Nov.; all coll. Hill; Sassafra, Oct., Tonnoir. Tasmania: Launceston (Cataract Gorge); Geeveston, Dec.; Bruny Is., Jan.; Cradle Valley, Jan.; Eaglehawk Neck, Nov.; Brown R., Dec.; all coll. Tonnoir. South Australia: Meadows, Aug., Swan. Western Australia: Pemberton, Aug., Ferguson, Nicholson; Kirup, Aug., Nicholson; Walgarup Brook, Aug., Nicholson.



Text-fig. 15.—Tarsi of *Austrosimulium* spp., females.

Biology: The full distribution has been given above, because this is a widespread though usually unrecognized species. The adults are apparently cryptic; Swan notes the South Australian specimens as biting man, and those collected by Skuse were presumably biting, otherwise the name is difficult to understand. The early stages are nearly always sparse, only a few specimens being found in any one locality at any one time. They prefer moderately fast, clear, shallow water, but may persist for a while when the flow has been considerably reduced. They are usually attached to vegetation.

AUSTROSIMULIUM VICTORIAE Roubaud.

Simulium victoriae Roubaud, 1906, p. 521. Type in British Museum, London.

Austrosimulium victoriae (Roubaud), Tonnoir, 1925, p. 240; Smart, 1945, p. 499.

Austrosimulium tasmaniense Tonnoir, 1925, p. 245. Type in Division of Economic Entomology, C.S.I.R., Canberra.

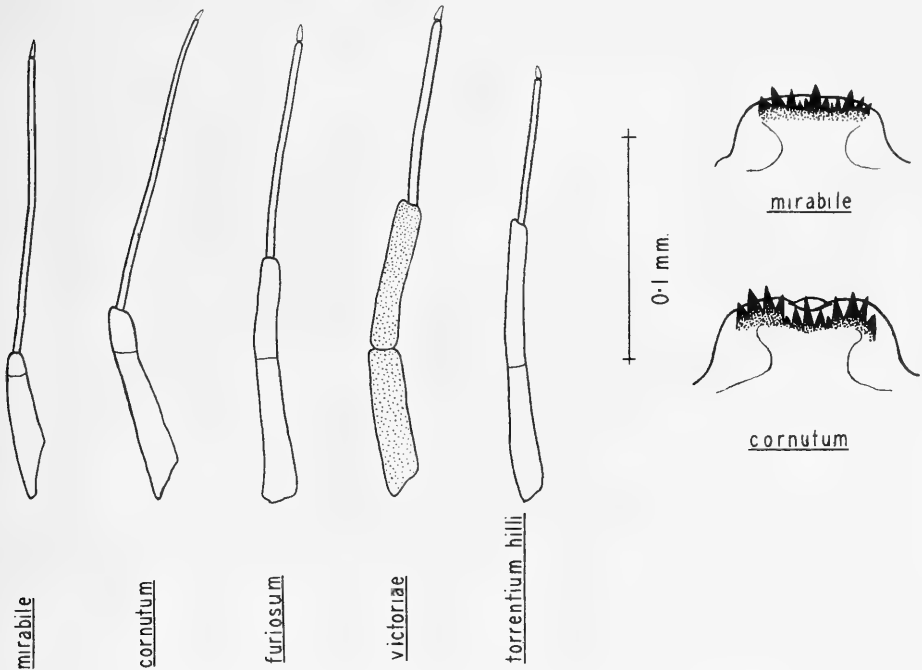
Female: A medium-sized, relatively long-bodied, uniformly dark species. Frons about one-quarter head width; antennae long (Fig. 17A); scutum very dark; propleural hairs present or absent; legs uniformly brown; calcipala a little more than half width of metatarsus (Fig. 15); abdominal tergites dull brown, not tomentose.

Male: Similar to *A. furiosum*.

Cocoon: Elongate oval, with a narrow collar, and distinguished from all other species by having two long, dorsal projections which curve downwards and inwards to cover the respiratory horns of the pupa. Tonnoir's notes suggest that Canberra specimens may have only a single, long, dorsal projection, like that of *A. cornutum*, but the material now available is too fragmented to be certain of this point.

Pupa: Respiratory horn rather long and somewhat flattened, the relatively short filaments being inserted along its edge and curved inwards in a characteristically formed tuft. The horn in mainland specimens is broader in the middle (Fig. 12) than in those from Tasmania, but the two are otherwise similar.

Larva: Easily recognizable by the dark brown to blackish basal segment of the antennae, all other species known to us having entirely pale antennae. Otherwise very like *A. furiosum*, but with a more robust anal sclerite. The gill-spot is, however, more like that of *A. bancrofti*, so full-grown larvae are easily identified.



Text-fig. 16.—Antennae of larvae of *Austrosimulium* spp., and submental plates of two spp.

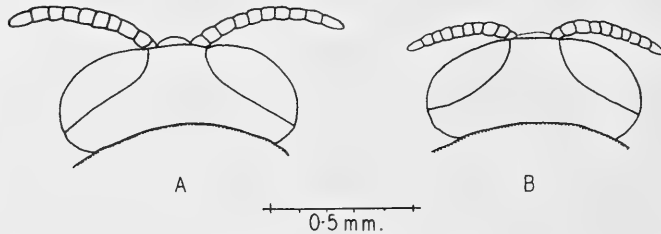
Synonymy.—A female in the School of Public Health and Tropical Medicine, bearing a label "Mts. of Victoria, 15.vii.1899, C. French, 1900.171", and identified by Roubaud in 1906 as *Simulium victoriae* Roub., proved to be exactly similar to *A. tasmaniense* Tonn., as recognized from Tonnoir's original series. We sent an inquiry to Mr. Paul Freeman of the British Museum, who was kind enough to give us the following reply:

"Roubaud in his original description refers to 'a number of females'. We have five females, all bearing exactly the same labels as the specimen referred to by yourself as collected by French in 1899 and identified by Roubaud in 1906 as *S. victoriae*. One of ours bears a type label, the others are presumably paratypes. There is no doubt at all

in my mind but that you have one of the same series and that yours is also a paratype. However, on examination, one specimen was seen to be different and is in fact a female of *Cnephia umbratorum*; the other four appear to be one species. We have also two paratypes of *Austrosimulium tasmaniense*: Edwards has placed them beside *A. victoriae* and put a query on the label below Tonnoir's species. I can see no difference whatsoever between these two species. The claws in *victoriae* are simple and therefore it cannot be *cornutum*. The abdomen is uniformly velvety-black and the calcipala between a half and two-thirds width of metatarsus, and it therefore fits *tasmaniense* and not *furiosum* or *torrentium*. Unfortunately we have no specimens of *furiosum* or *torrentium* in the collection, so I am quite unable to compare them, but there seems to be little doubt that *tasmaniense* is the same as *victoriae*."

Distribution.—Tasmania: Cradle Valley, Jan.; St. Patrick's R., Oct.-Nov.; Mt. Wellington, Nov.; Brown R., Dec.; National Park, Dec.; Geeveston, Dec.; Hartz Mts., Dec.; Mt. Field, Dec.; all coll. Tonnoir. Victoria: "Mts. of Victoria", July, French (*type locality*); Mt. Buffalo, Oct., R. J. Tillyard and G. A. Currie. New South Wales: Mt. Kosciusko (The Creel, Diggers Ck., Sawpit Ck.), Dec., Tonnoir, Mackerras; Wentworth Falls, Mar., Wharton. A.C.T.: Black Mt., June, Hill; Molonglo R., Sept.-Oct.; Cotter R., Sept.-Oct.; Blundell's, Nov.; Condor Ck., Oct., Hill and J. W. Evans; all coll. Tonnoir except first and last.

Biology: Tonnoir took females flying round him but not biting. The early stages were mostly found on stones, occasionally on grass-blades, in small to medium-sized creeks with only a moderate flow of water (Tonnoir).



Text-fig. 17.—Heads of A: *A. victoriae*, and B: *A. torrentium hilli* (both specimens from A.C.T.); dorsal view, to show relative lengths of antennae.

AUSTROSIMULIUM TORRENTIUM TORRENTIUM Tonnoir.

Austrosimulium torrentium Tonnoir, 1925, p. 247; Smart, 1945, p. 499. Type in Division of Economic Entomology, C.S.I.R., Canberra.

Female: A small, compact, greyish species. Frons one-third of head width; antennae (Figs. 1, 17B) distinctly shorter than vertical length of head, basal two segments bare and a lighter brown than remainder. Scutum grey; pleurae with marked ashy sheen. Legs fawn, usually with darker knees and some darker suffusion towards ends of segments. Abdomen with tergites brown, sometimes dark, but not velvety.

Male: Third antennal segment not much longer than fourth, calcipala barely half width of metatarsus, otherwise as *A. furiosum*. Style of hypopygium with two, sometimes three, spines; posterior part of phallosome with a patch of denticles ventrally on each side.

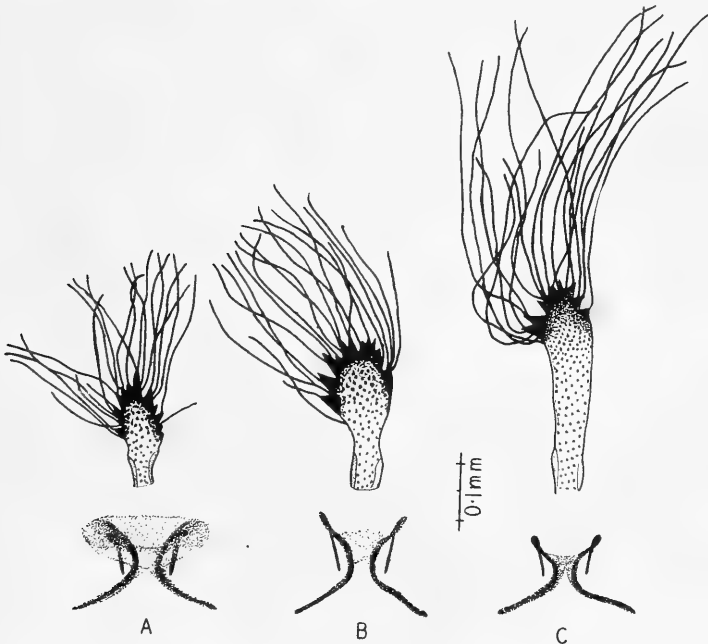
Cocoon: Flat, rounded, with a narrow, raised, central part to contain the body of the pupa, and with a small, oval opening into which the head and anterior part of the pupal thorax fit neatly; margin of opening with thickened, rolled edge.

Pupa: Remarkable for the flattened head and anterior part of the thorax, adapted to fit exactly to the aperture in the cocoon, with only the respiratory apparatus projecting beyond its general surface. Horn very short, broad, orange basally, black distally, where it is armed with stout black spines (Fig. 18A). The filaments are short, fine, 15-20 in number, and arise from the distal end of the horn. The thorax bears on each side a raised, blunt tubercle just behind the base of the respiratory horn, and a stout, dark, backwardly directed spine over the post-alar area of the underlying adult. These structures are present in all the races of *A. torrentium*, but we have not seen them in any other species.

Larva: Antennae with distal segment only about half the length of the basal; margin of submentum evenly curved; anal sclerite stout, with a somewhat irregular, brown, chitinous expansion of its anterior limbs (Fig. 18A). The gill spot shows the black spines even at an early stage of development, and, when fully formed, has the perfect form of the pupal horn, with the filaments curved in an anterior tuft.

Distribution.—Tasmania: St. Patrick's R., Nov. (*type locality*); Burnie (Emu R.), Oct., Feb.; Launceston (Cataract Gorge), Oct.-Jan.; Cradle Valley, Jan.; Mt. Farrel, Feb.; all coll. Tonnoir.

Biology: Adults have been taken by sweeping plants. The early stages were found in larger streams with a very swift flow, to which the form of the cocoon and pupae seem specially adapted. Tonnoir notes that the prepupal larvae seek indentations in the stones, "which the cocoon closes like a flat lid". We have not seen a similar adaptation to unusually fast water elsewhere in the family, even in *A. pestilens*.



Text-fig. 18.—Pupal horns and anal sclerites of races of *A. torrentium*.
A: *A. torrentium torrentium*; B: *A. torrentium* var.; C: *A. torrentium hilli*.

AUSTROSIMULIUM TORRENTIUM HILLI, n. subsp.

Mainland specimens fall in two groups, both differing from Tasmanian specimens in larval characters, and one also in pupal characters. The differences appear to be constant, and we propose to associate the name of our friend, Mr. G. F. Hill, with the more distinctive of the two.

Adult: Female rather lighter in general colouration, otherwise both sexes similar to typical subspecies.*

Cocoon: Smaller and more oval than typical subspecies; opening egg-shaped, margin smooth and only slightly thickened. Tonnoir notes that cocoon is covered in life with a gelatinous material, which gives it a milky appearance.

* Propleural hairs were absent in *torrentium* (two specimens), present in *hilli* (four specimens), and present in nine, absent in eight of the females associated by Tonnoir with the variant described below. An analysis of the propleural hairs in further accurately associated series of the three forms might be interesting.

Pupa: The flattened head and thorax, general habitus, and armature as in typical subspecies. Respiratory horn about twice as long and not so broad (Fig. 18C), coloration as in typical subspecies, but apical spines fewer and weaker. Filaments slender, about 30 in number.

Larva: The anal armature (Fig. 18C) is relatively delicate, and there is no trace of the chitinous expansion of the anterior limbs, which is characteristic of the typical subspecies. Gill-spot with stem long, as in pupa, and spines relatively inconspicuous. The margin of the submental plate is scalloped (like *A. cornutum*, Fig. 16), but the antennae, cirlet, and ventral papillae are as in typical subspecies.

Types: We feel it necessary to follow the unusual course of designating a full-grown "gill-spot" larva from Cotter R., A.C.T., 10 Oct., '29, Tonnoir, as holotype. Morphotype pupa, adult female, and adult male have been selected from the same series. All types are in the collection of the Division of Economic Entomology, C.S.I.R., Canberra.

Distribution.—A.C.T.: Cotter R., Oct.-Nov. (*type locality*). New South Wales: Yarrangobilly R. (near Caves), Feb.; Mt. Kosciusko, Thredbo R., Dec., Snowy R., Feb. All coll. Tonnoir.

Variation: The second form mentioned above links *hilli* with *torrentium*, though in a distinct step without intermediate grading. The anal sclerite of the larva (Fig. 18B) and submental plate are similar to those of *hilli*, but the pupal respiratory horn (and consequently the gill-spot of the larva) is short, broad, with strong spines, like a more than usually robust *torrentium*. Cocoon more like typical subspecies, often asymmetrical. In short, adults and young larvae cannot be separated from *hilli*, pupae are identical with *torrentium*, and only the full-grown "gill-spot" larva is definitely recognizable as a separate entity. Tonnoir had carefully linked bred series from Cotter R., Oct. (in company with the type series of *hilli*) and the Cotter-Murrumbidgee Junction, Oct. There are specimens also from Cotter R., Sept.-Nov.; Five Fords, Dec.; Mt. Kosciusko (Digger's Ck., Thredbo R.), Dec.; all coll. Tonnoir.

The status of the three forms is difficult to assess. We have been conservative, but possibly they are sibling species, which have diverged sufficiently not to breed together when they meet (as the two mainland forms do in the Cotter R.).

Tonnoir (MS.) noted an abnormality in about 5 per cent. of the males of the "short-horned" variant, the scutum being shining grey, the hind metatarsi more incrassate than normal, and the size and distribution of the enlarged facets of the eye differing from normal. He queried these abnormal males as possibly gynandromorphs. A pinned specimen in the collection has female scutal and leg coloration, but is a male in other respects; the spirit material, unfortunately, had dried.

Biology: Habits of adults unknown. Early stages in swift, clear water, apparently occupying the same type of situation as the typical form.

NEW ZEALAND SPECIES.

We have nothing to add to Tonnoir's descriptions so give only brief notes on the New Zealand species.*

AUSTROSIMULIUM VEXANS (Mik).

Tonnoir, 1925, p. 250. Known only from female; has toothed claws. Auckland Is. (*type locality*).

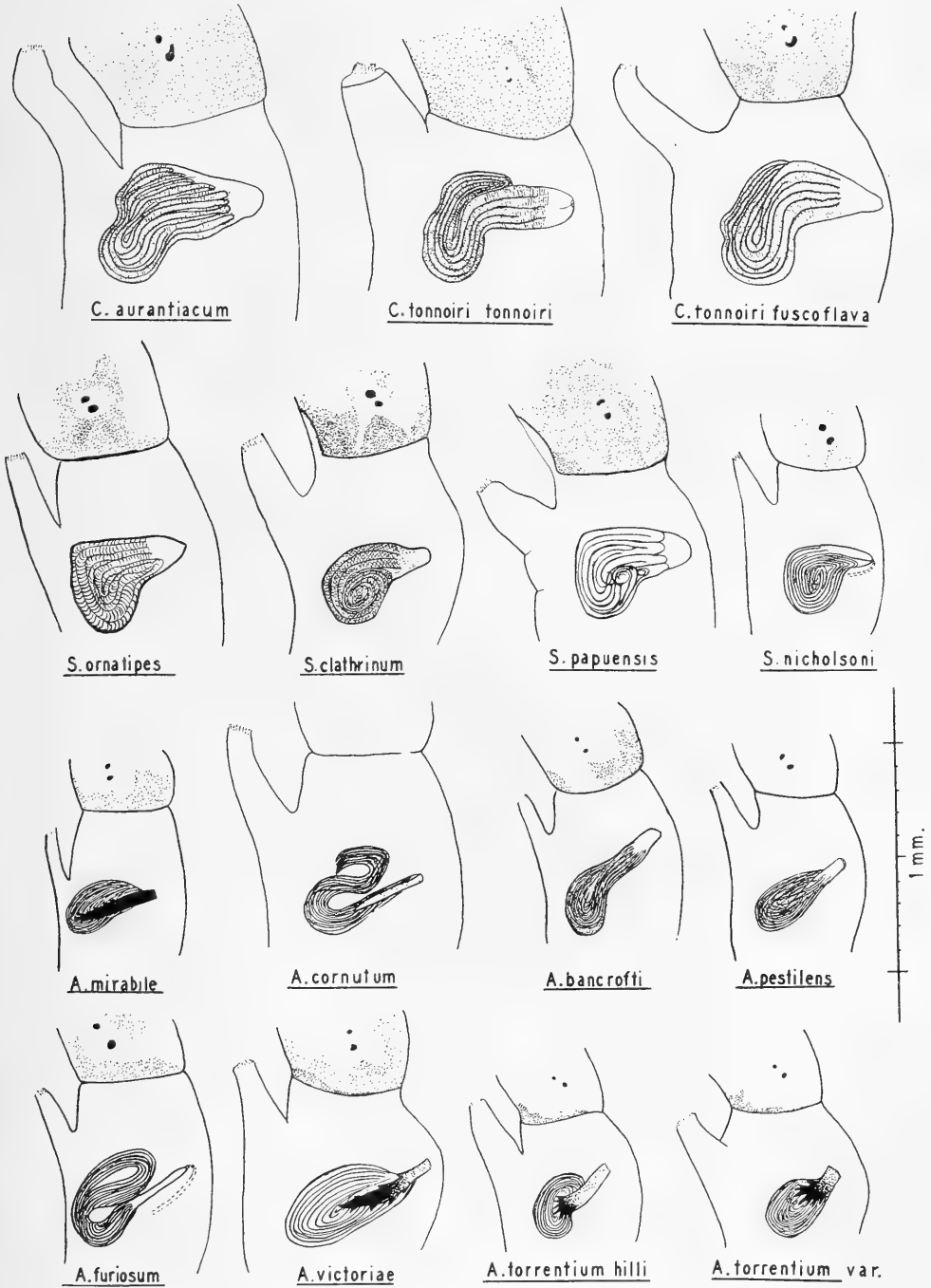
AUSTROSIMULIUM UNGULATUM Tonnoir.

Tonnoir, 1925, p. 250. Known only from female; has toothed claws; a fierce biter. South Island (Reefton, *type locality*).

* To complete the list, it should be mentioned that Edwards (1931, pp. 143 and 144) records *Austrosimulium anthracinum* (Bigot) and *A. moorei* (Silva) from Patagonia and Chile. Both are known only from adult females.

AUSTROSIMULIUM AUSTRALENSE (Schiner).

Tonnoir, 1925, p. 251. Genotype of *Austrosimulium*. Larva, pupa, cocoon, female and male known. A small, unadorned species with simple female claws; appears to be a

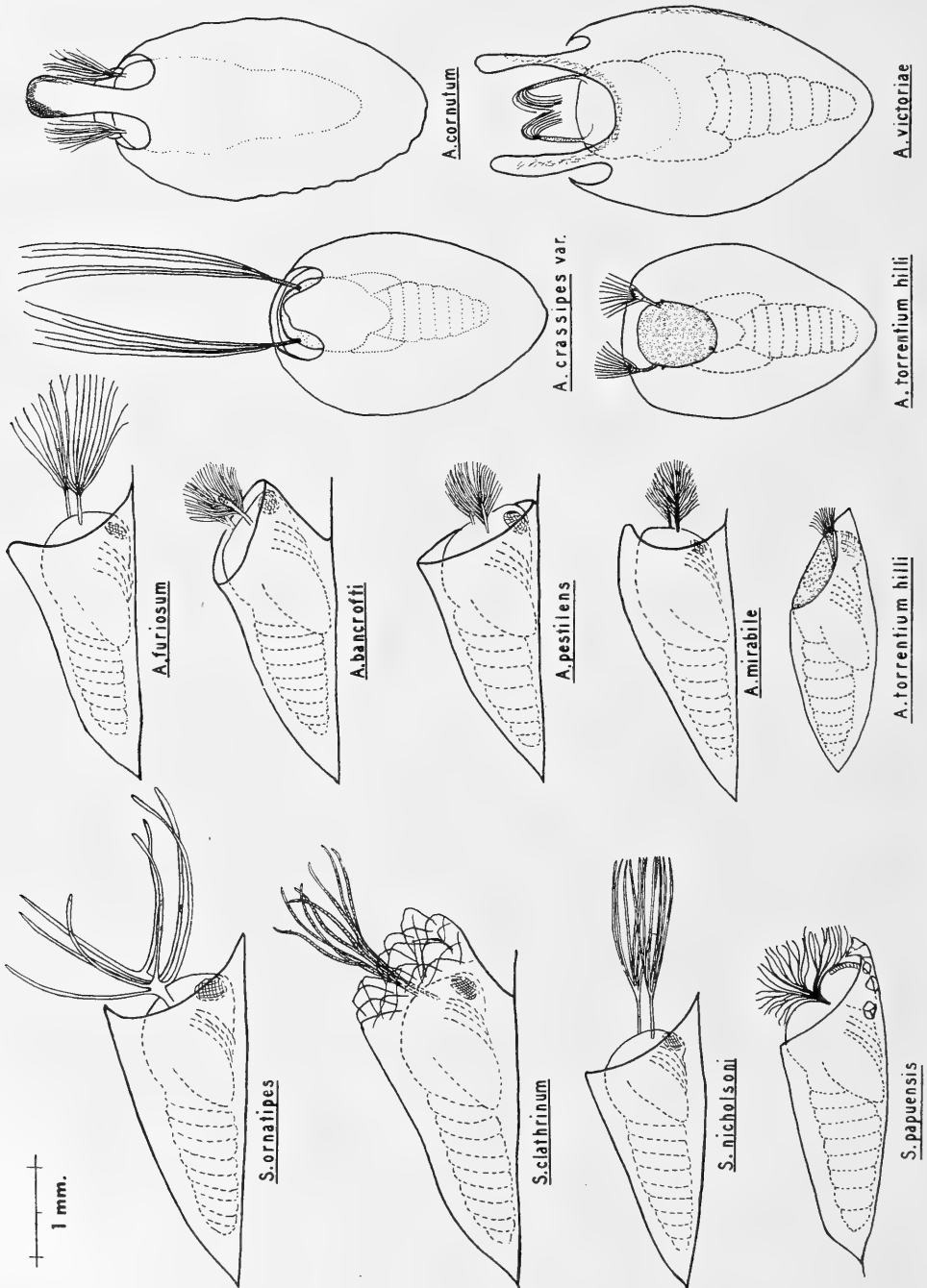


Text-fig. 19.—Lateral view of full-grown larvae, showing gill-spots.
 (For *A. crassipes* see Fig. 13D; for *papuensis* read *papuense*.)

fairly central member of the genus on the characters of all stages. Bites man. North Island (Auckland *type locality*), South Island.

AUSTROSIMULIUM TILLYARDI Tonnoir.

Tonnoir, 1925, p. 253. Larva, pupa, cocoon, female and male known. A small, undistinguished species with simple claws, but with an unusual pupal respiratory organ which may provide a link with other genera. Not known to attack man. North Island, South Island (Nelson *type locality*).



Text-fig. 20.—Cocoons and pupae. For *Cnephia* type, see Fig. 11.
(For *papuensis* read *papuense*.)

AUSTROSIMULIUM LATICORNE Tonnoir.

Tonnoir, 1925, p. 253. Larva, pupa, cocoon, female and male known. Distinguished from *A. tillyardi* only by pupal respiratory organ. Not known to attack man. South Island (Waiho type locality).

AUSTROSIMULIUM MULTICORNE Tonnoir.

Tonnoir, 1925, p. 254. Larva, pupa, cocoon, female and male known. Distinguished from above only by pupal respiratory organ. Not known to attack man. North Island, South Island (Mt. Arthur type locality).

AUSTROSIMULIUM LONGICORNE Tonnoir.

Tonnoir, 1925, p. 254. Larva, pupa, cocoon, female and male known. Only distinguished from above by the remarkable pupal respiratory organ which, like that of *A. tillyardi*, may link with other genera. Not known to attack man. North Island, South Island (Kaikoura type locality).

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NEW SPECIES OF SIMULIIDAE (DIPTERA, NEMATOCERA) FROM
NEW SOUTH WALES.

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(Twenty-one Text-figures.)

[Read 27th October, 1948.]

INTRODUCTION.

Unfortunately the following information could not be included in the "Revisional Notes on Australasian Simuliidae (Diptera)", by I. M. and M. J. Mackerras (these PROCEEDINGS, lxxiii, p. 372, and is given here to complete our present knowledge of the Australasian Simuliidae. One new species of *Simulium* is described, additional notes are made on *Austrosimulium crassipes* Tonnoir, including an account of the female and immature stages, and an unknown Simuliid larva is described.

SIMULIUM MELATUM, n. sp.

Types.—Pinned holotype female and allotype male in the Macleay Museum, University of Sydney. Morphotype larva and pupa and one male paratype mounted on slides, larval and pupal specimens in alcohol also in the Macleay Museum. One female paratype, larvae and pupae in the Queensland Institute of Medical Research.

Type Locality.—Lett River, Hartley, Blue Mountains, New South Wales (Wharton, January, 1948).

DISTINCTIVE CHARACTERS.

This species belongs to the *clathrinum* group of the genus *Simulium* as defined by M. J. and I. M. Mackerras. From all described Australian species *S. melatum* may be distinguished as an adult by the completely dark legs; in all other species the first hind tarsi have a broad pale band. *S. oculata* Enderlein is the only New Guinea species with which it could be confused, but the silver scales of *S. melatum* on the frons, mesonotum, and sides of the abdomen should differ from the golden-yellow and metallic-yellow pubescence of *S. oculata*. In addition, the enlarged upper facets of the eye in the male *S. oculata* are stated to have a diameter greater than the diameter of the antennal flagella segments; in *S. melatum* these facets have little more than half the diameter of the antennal segments.

The pupa and cocoon together are distinct. The pupa resembles *S. clathrinum* and *S. ornatipes* in that each respiratory organ consists of four filaments arising from a short base. These filaments, however, are intermediate in size between the smooth, very stout filaments of *S. ornatipes* and the relatively smooth, slender filaments of *S. clathrinum*. Furthermore, the filaments have a coarse, granulated, irregularly wrinkled appearance. The cocoon is similar to that of *S. ornatipes*, but the dorsal projection is longer in *S. melatum*.

The larva, with dark pigmentation on most of the head capsule, simple rectal gills and the absence of ventral papillae differs from any known Australasian *Simulium* and on key characters could only be confused with *Cnephia* species, from which it can be easily separated on the form and number of teeth in the anal circlet.

DESCRIPTION.

Female.

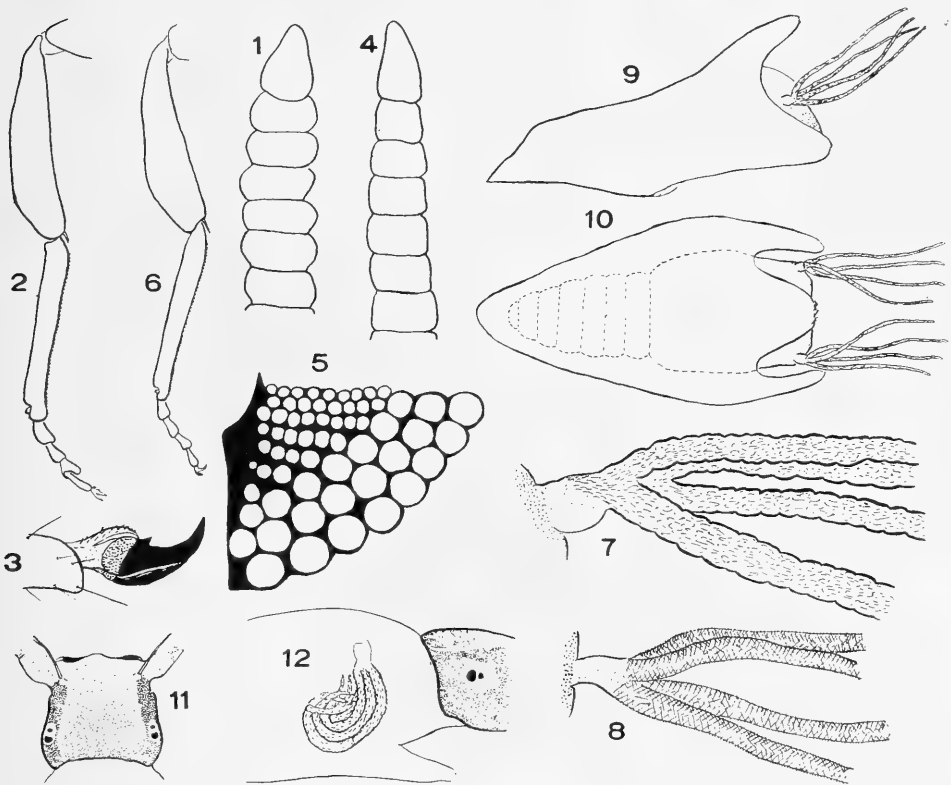
Length: 2.25 mm.; wing 2 mm.

Head.—The vertex and occiput are dull black and sparsely covered with silver-grey hairs. The frons is grey with a silver-grey pubescence, the frons slightly longer than

wide and between one-quarter and one-third of the maximum width of the head. The antennae (Text-fig. 1) are composed of eleven segments, of which the basal two are brown and the remainder dark brown to black, with a fine grey pubescence. The palpi are normal for the group.

Thorax.—The mesonotum is black with a covering of fine silver scales. The pleura are dull black and bare, except for a patch of silver scales on the membranous (prealar) area behind the mesothoracic spiracle, a group of longer silver scales on the propleuron and a patch of pale bristles on the lower sterno-pleuron. The scales on the scutellum are silver and the halteres are dark brown at the base with cream knobs.

Legs (Text-fig. 2).—The legs are almost uniformly dark brown to black with only the bases of the tibiae light brown and a faint suggestion of a lighter colour in the form of a broad band on the first hind tarsi. The hairs on the legs are normal, many short dark brown hairs on all segments, striated scales on the femora and tibiae which



Text-figures 1-12.

Figs. 1-6 and 9-12. *Simulium melatum*, n. sp. Female: 1, antennal flagellar segments $\times 175$; 2, hind leg $\times 40$; 3, tarsal claws $\times 175$. Male: 4, antennal flagellar segments $\times 175$; 5, facets of eye $\times 175$; 6, hind leg $\times 40$. Pupa and cocoon $\times 8$: 9, lateral view; 10, dorsal view. Larva: 11, head, dorsal view $\times 25$; 12, gill spot $\times 25$. Basal portion of pupal respiratory organ $\times 50$: 7, *S. melatum*; 8, *S. clathrinum*.

glisten with direct lighting, and elongated hairs on the fore and hind tarsi. There do not appear to be any particular regions where the hairs show distinctive colouring. The hind tibiae are slightly angulated and longer than the first hind tarsi. The calcipalus is from half to two-thirds of the width of the first hind tarsus and the pediculus is clearly defined. A very small basal tooth is present on the tarsal claws (Text-fig. 3).

Wings.—At the wing base the veins are dark and the wing-membrane is clouded. The venation and distribution of macrotrichia are normal for the group.

Abdomen.—There are a few silver scales on the first and second tergites, but the remainder of the scales on the dorsal surface of the abdomen are dark brown. At the junction between the dorsal and lateral margins of the abdomen there is a distinct line where the dark scales of the dorsal surface are replaced largely by silver-grey scales, particularly on the second, third, fourth and fifth segments. These lighter scales thin out towards the ventral surface, which is almost bare and grey in colour.

Male.

Length 2.3 mm.; wing 2 mm.

Head.—The clypeus is black, appearing frosted in some lights but with no silver-grey pubescence as in the female. The antennae have all the segments dark brown to black, with only the junctions between the first and second segments a lighter brown; in addition the flagella segments appear to be relatively longer than in the female (Text-fig. 4). The enlarged upper facets of the eye (Text-fig. 5) have approximately the same diameter as those of *S. nicholsoni* M. J. and I. M. Mackerras, and thus are smaller than those of *S. clathrinum* M. J. and I. M. Mackerras and *S. papuensis* Wharton.

Thorax.—The scales on the mesonotum, though in most lights silver, may sometimes appear golden, whereas in the female these scales are always silver.

Legs.—The hind tibia is more enlarged and more angulated (Text-fig. 6) than in the female; otherwise the legs are similar in both sexes.

Abdomen.—Similar to that of the female, but the dark scales on the dorsal surface extend further down the lateral surfaces and, when replaced by the silver scales, these scales are not as numerous as in the female.

Genitalia.—The genitalia do not appear to show any distinctive features.

Pupa.

Length about 4 mm. Dark brown in colour.

The pupa resembles *S. clathrinum* in all details except the form of the respiratory organs, which consist of four elongated dark filaments arising from a short, light brown base. The filaments are relatively longer and stouter than those of *S. clathrinum* and the surface of the filaments has a coarse, irregularly wrinkled appearance (Text-figs. 7 and 8).

Cocoon.

A typical wall pocket type, resembling *S. ornatipes* Skuse in having a median dorsal projection which reaches the base of the pupal respiratory organs (Text-figs. 9 and 10). No anterior collar is present and texture of the cocoon is about the same as in *S. clathrinum*.

Larva.

Length 5–6 mm. Robust. Head dark, thorax and abdomen grey.

Head (Text-figs. 11 and 12).—The pigmentation of the fronto-clypeus is uniformly heavy along the posterior margin, gradually becoming less obvious towards the anterior margin, where pigment is usually lacking. Except for a small area around the eyes the lateral and ventral surfaces of the head are almost uniformly dark. The ventral fissure is well marked but not as deep as in *S. papuensis*. In other respects the head is similar to other members of the *clathrinum* group.

Thorax.—The gill spot (Text-fig. 12) is closest to *S. clathrinum* but is larger, and the coarse, wrinkled appearance of the filaments is again distinctive.

Abdomen.—The anal sclerite is normal, with no backwardly directed strut, but the rectal (anal) gills are simple; ventral papillae are absent, though ventro-lateral swellings, as in *S. clathrinum*, may be present. The anal cirlet consists of some seventy to eighty rows of hooks, each row with twelve or thirteen hooks.

Biology.—The early stages have been collected from grass blades in swiftly running, clear water, together with the early stages of *S. ornatipes*, *Austrosimulium furiosum* and *A. bancrofti*. Early stages have also been found in large numbers on the surface of rocks in small streams at the point where the flow is the greatest; in these cases *S. melatum* has been the only species present. No adults have been collected, sweeping the surrounding vegetation having given no results.

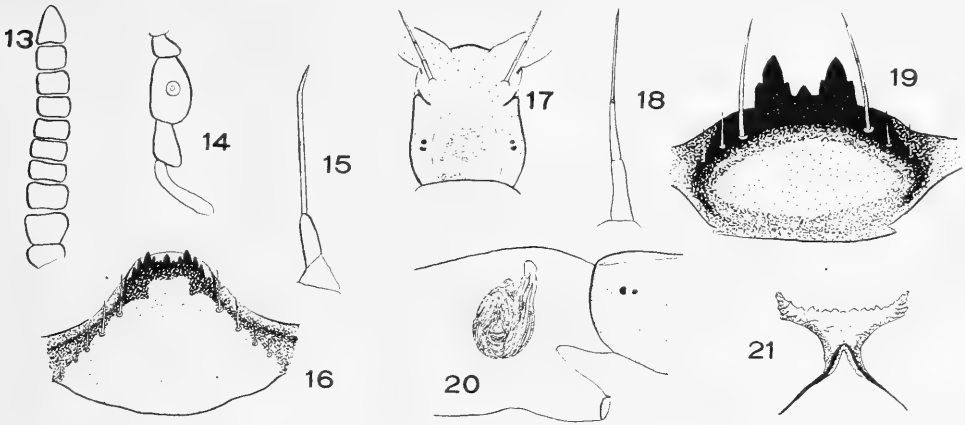
Distribution.—New South Wales, Blue Mountains district, Hartley, December, January and March; Mount Victoria, March. Sydney district, Oxford Falls, November. All specimens collected by author.

AUSTROSIMULIUM CRASSIPES Tonnoir.

As stated by Mackerras (1948), I have recently found the early stages of an *Austrosimulium* species, the male of which is very similar to Tonnoir's unique male type of *A. crassipes*. It seems likely that when the female and immature stages of Tonnoir's species have been taken at the type locality in Victoria they will conform with the following description. As the distinctive characters have already been outlined by Mackerras only such additional notes as may be needed to give a positive identification have been added.

Types.—Male type in Division of Economic Entomology, C.S.I.R., Canberra. Allotype female and paratype male, morphotype larva, pupa and cocoon, together with larvae and pupae, in the Macleay Museum, University of Sydney.

Type Locality.—Sassafras, Victoria (Tonnoir, 1922). Allotype female and immature stages collected at Fairy Bower, Mount Victoria, New South Wales (Wharton, January, 1948).



Text-figures 13-21.

Figs. 13-16. *Austrosimulium crassipes* Tonnoir. 13. Female antenna $\times 65$. 14. Female palpus $\times 65$. 15. Larval antenna $\times 65$. 16. Larval labium $\times 175$.

Text-figs. 17-21. Unknown Simuliid larva. 17. Head, dorsal view, $\times 25$. 18. Antenna $\times 175$. 19. Labium $\times 175$. 20. Gill spot $\times 25$. 21. Anal armature $\times 175$.

DESCRIPTION.

Female.

Length 2.4 mm.; wing 2.5 mm.

Head.—The frons, vertex and occiput are grey with a silver pubescence, the frons about one-third of the maximum width of the head and longer than wide. The second segment of the antenna is brown, the third and flagellar segments dark brown to black, the flagellar segments with grey pubescence. The size and shape of the various antennal segments are as illustrated (Text-fig. 13). The palpi are black, the two basal segments small, the third swollen, longer than the fourth, which is half the length of the thin, elongated terminal segment (Text-fig. 14).

Thorax.—The mesonotum is black with relatively long creamy-yellow hairs, which are uniformly distributed over the scutum to the base of the scutellum, which is black, with only a few scattered yellow hairs on its surface. The pleura are dark brown to black, but certain regions, particularly the anepisternum and lower sternopleuron, show grey reflections. Propleural hairs are absent, the upper mesepimeral hairs are dark, and a single dark hair on the sternopleuron is visible.

The postnotum is black and the halteres have a dark brown base with a broad pale cream knob, the pale colouring extending downwards on one side of the stem.

Legs.—Completely dark, but the femora and tibiae bear some yellow hairs in addition to the normal dark brown to black hairs. The fore and mid legs are of normal size, the femur and tibia equal in length in the fore legs, the tibia slightly longer than the femur in the mid legs. The femur, tibia and first hind tarsus of the hind leg are all swollen, and the tarsus is distinctly curved (Mackerras, 1948, Text-fig. 13B). The calcipalus is large, almost as wide as the metatarsus, but separated from it by a slight notch. The pedisulcus is well defined and all the tarsal claws bear a strong basal tooth.

Wings.—The wing venation is normal, the wing membrane at the base is clouded and the main veins are dark brown.

Abdomen.—Long creamy yellow hairs are present on the lateral margins of the first segment, otherwise the abdomen is completely dark brown to black with only scattered fine dark brown and yellow hairs on all segments.

Male.

Length 2.4 mm.; wing 2.5 mm.

The male description follows that given by Tonnoir, with the following additions and distinctions.

Head.—The second antennal segment is similar to that of the female, definitely lighter in colour than the remaining segments. The incrassate third segment of the palpus is slightly longer than the fourth, which is a little more than half the length of the elongated fifth segment.

Thorax.—The mesonotum is darker than in the females, as also are the halteres which are dark up to and including the basal portion of the knob.

Legs.—The tarsi of the fore leg are equal in length to the tibia, which is itself equal to the femur. The mid leg tarsi are distinctly longer (subequal according to Tonnoir) than the corresponding tibia and femur, which are again equal. The first hind tarsus is very characteristic, more swollen than in the female, though not quite as incrassate as in Tonnoir's type male (Tonnoir, 1925, fig. 2 (I); Mackerras, 1948, Text-fig. 13A).

Abdomen.—Similar to that of the female, but more yellow hairs are present.

Pupa.

Length about 3 mm. Light brown in colour.

The surface of the cephalothorax bears minute granules which are larger and darker around the base of the respiratory organs and on the head region. The thoracic notum carries a pair of short, stout curved bristles on either side of the mid-line and a long hair at the base of the respiratory organ. These organs are characteristic (Mackerras, 1948, Text-figs. 12 and 20).

On the dorsal surface of the abdomen six subapical hooks are present on each of the third and fourth segments. Ventrally there are four subapical spines on the fifth, two on the sixth and two on the seventh segments. The terminal spines are comparatively large, upwardly and inwardly directed.

Cocoon.

A typical *Austrosimulium*, finely woven, neatly formed and incomplete beneath the abdomen of the pupa (Mackerras, 1948, Text-fig. 20).

Larva.

Length 4–5 mm. Head light brown, thorax and abdomen grey.

Head.—The posterior margin of the head capsule is ringed with dark pigment, otherwise, apart from a median longitudinal interrupted band and a pair of submedian circular patches, the head is only lightly segmented (Mackerras, 1948, Text-fig. 13E). The slender second segment of the antenna (Text-fig. 15) is twice the length of the stout basal segment and the antenna is distinctly longer than the base of the mouth fan. The submentum consists of thirteen teeth with five hairs laterally placed on either side (Text-fig. 16).

Thorax.—The gill spot (Mackerras, 1948, Text-fig. 13D) is distinctive, with a pale base and six filaments, which are coiled anterior to the base in a remarkably even manner.

Abdomen.—The rectal gills are simple and a pair of ventral papillae (basal tubercles) are present on the last segments. The anal armature (Mackerras, 1948, Text-fig. 9) possesses a backwardly directed strut and a chitinous rod which encircles the abdomen beneath the anal sclerite—the ends of the ring are tapered off to end just below the posterior arms of the anal sclerite. The anal circling consists of about ninety rows of hooks, each row containing 12 to 15 teeth.

Biology.—The larvae were collected on leaves and the pupae on stones in small mountain streams. The immature stages were not numerous and have been found in company with *A. victoriae*, *A. furiosum* and an unknown Simuliid larva.

Distribution.—Sassafras, Victoria; Mount Victoria and Wentworth Falls, Blue Mountains, New South Wales.

SIMULIID LARVA.

Genus and Species Unknown.

To assist subsequent collectors, the description of a single larva, collected at Engineer's Cascade, Mount Victoria, New South Wales, in company with the immature stages of *A. crassipes* Tonnoir is here undertaken. The larva shows affinities with larvae of the genus *Cnephia* and the genus *Simulium*, and may possibly be the larva of one of the described species belonging to *umbratorum* group of the genus *Cnephia*. The submentum is the most characteristic feature of the larva in that it consists of only three conspicuous teeth.

Description of Larva.

Length 5.7 mm. Head light yellow-brown, thorax and abdomen yellowish.

Head (Text-fig. 17).—The head is distinctly longer than broad, at no point is the capsule heavily pigmented, but the posterior margins and a median longitudinal region on the frontoclypeus are darker than the remainder. The eyes are small, the anterior pair circular in outline, the posterior pair slightly larger and again circular, but with the anterior margin flattened. The antennae (Text-fig. 18) are slightly longer than the base of the mouth fan—the basal segment almost one and a half times the length of the second segment. The submentum (Text-fig. 19) consists of three teeth, an extremely large tooth on each side with clearly defined shoulders and a much smaller simple median tooth. In addition three bristles, one large and two small, are present lateral and posterior to the outer tooth on each side.

Thorax.—The gill spot (Text-fig. 20) is dark with a yellow base and is oval in shape. The filaments are coiled posterior to the main stem in a manner typical of the genus *Simulium*. When dissected the future respiratory organ appears to consist of twelve extremely long, slender filaments arising from four main stems, i.e. the form found in the genus *Cnephia*.

Abdomen.—No rectal gills are visible. The anal sclerite (Text-fig. 21) is well developed but does not possess backwardly directed struts. The anal circling consists of about fifty rows of hooks, each row containing 10–13 hooks. Ventral papillae are present and clearly defined.

ACKNOWLEDGMENTS.

The financial assistance of the Commonwealth Research Grants Committee which made possible the collection of material and the advice of Dr. I. M. Mackerras, Queensland Institute of Medical Research, is gratefully acknowledged.

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OBSERVATIONS ON THE COMPARATIVE SURVIVAL OF VARIOUS STAGES OF
 AÆDES (STEGOMYIA) SCUTELLARIS WALKER AND AÆDES (STEGOMYIA)
 AEGYPTI LINNAEUS AT VARYING TEMPERATURES AND HUMIDITIES.

By A. R. WOODHILL,
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[Read 27th October, 1948.]

The mosquito *Aedes (Stegomyia) scutellaris* Walker* has recently been demonstrated (Mackerras, 1946) to be the common vector of dengue fever in the territory of Papua-New Guinea. The vector of this disease in Australia is the cosmopolitan species, *Aedes aegypti* Linnaeus, which has been recorded as far south as southern New South Wales. A form, possibly a new sub-species, of *Aedes scutellaris* has, however, been recently recorded in the Northern Territory of Australia, and it becomes a matter of interest whether *Aedes scutellaris*, if accidentally introduced into Queensland and New South Wales, could establish itself there and become an important dengue vector.

The following experiments were designed to give some information on the relative viability of *A. aegypti* and *A. scutellaris* under winter and summer conditions in Sydney, and also under colder conditions which would obtain in exposed situations in inland New South Wales during the winter.

EGGS.

As is well known, the eggs of some species of *Aedes* will remain viable in a dry state for long periods, up to twelve months in the case of *Aedes aegypti*. Recent work in New Guinea (Penn, 1947, and Forbes and Horsfall, 1946) has shown that the eggs of *Aedes scutellaris* when removed from water will remain viable for 42 to 61 days if kept damp or in a moist chamber, provided that they have remained on a wet surface for 48 hours after deposition, i.e. long enough for the embryo to develop its external features.

Table 1 shows the percentage hatching of eggs of *A. aegypti* and *A. scutellaris* removed from a wet surface at 80°F. after two days and allowed to dry out under natural outdoor conditions but protected from rain. Records were kept of the daily maxima and minima of temperature and humidity, and the mean daily records and also the extremes are given for each period. In addition, several lots of eggs were kept under controlled conditions with a constant temperature of 80°F. and relative humidity varying between 70% and 80%. The experiments were designed to cover the period from mid-winter to mid-summer in the Sydney district. While the winter was fairly normal, the spring and summer were exceptionally humid, and the extremely dry, hot conditions which often occur in this locality were not experienced. To determine the percentage hatching at the end of each period the eggs were immersed in water at 80°F. and observed for 14 days in order to record any delayed hatching.

It will be seen from Table 1 that no eggs of *A. scutellaris* hatched after exposure to outside conditions for periods of two to three months during winter, spring and early summer, whereas *A. aegypti* under similar conditions gave a percentage hatching from 46% to 83%. During the warmer and moister period of the year, however (experiments 19 to 26), a small hatch, varying from 4% to 10%, was obtained from *A. scutellaris*, while *A. aegypti* gave a hatch of 74% to 91%. Under what could be considered optimum conditions (constant temperature of 80°, humidity 70% to 80%) in the warm room *A. scutellaris* gave a hatching percentage of from 5% to 20% and *A. aegypti* 58% to 90%.

* See Stone, 1947, for nomenclature and taxonomy.

In addition to the natural temperatures shown in Table 1, various batches of eggs were exposed to temperatures of 30°F. to 40°F., such as could be experienced in the colder portions of the State, for varying periods. In all cases the humidity was kept up to 90% to 100% and the temperature was constant to within $\pm 1^\circ\text{F}$. unless otherwise

TABLE 1.
Percentage Hatching of Eggs of A. aegypti and A. scutellaris.

One hundred eggs in each experiment. Temperature and humidity figures=average daily maximum, average daily minimum, maximum for period and minimum for period in that order.

No. of Experiment.	Period.	Temperature. ° F.	Humidity. %	Percentage Hatched.	
				<i>A. aegypti.</i>	<i>A. scutellaris.</i>
1	81 days, 18th June to 7th September.	61, 48, 76, 41.	83, 43, 100, 20.	74	
2	" "	" " " "	" " " "		0
3	" "	80 constant.	70-80 constant.	74	
4	" "	" "	" "		20
5	87 days, 12th September to 8th December.	71, 58, 83, 50	87, 48, 100, 19.	83	
6	" "	" " " "	" " " "	69	
7	" "	" " " "	" " " "	48	
8	" "	" " " "	" " " "		0
9	" "	" " " "	" " " "		0
10	" "	" " " "	" " " "		0
11	" "	80 constant.	70-80 constant.	82	
12	" "	" "	" "	58	
13	" "	" "	" "		5
14	" "	" "	" "		12
15	69 days, 1st October to 8th December.	72, 60, 83, 54.	87, 49, 100, 19.	46	
16	" "	" " " "	" " " "		0
17	" "	80 constant.	70-80 constant.	90	
18	" "	" "	" "		14
19	84 days, 1st December to 23rd February.	77, 65, 90, 56.	94, 58, 100, 29.	74	
20	" "	" " " "	" " " "	78	
21	" "	" " " "	" " " "	82	
22	" "	" " " "	" " " "	91	
23	" "	" " " "	" " " "		10
24	" "	" " " "	" " " "		7
25	" "	" " " "	" " " "		4
26	" "	" " " "	" " " "		5

stated. As before, the eggs were allowed to develop on a wet surface at 80°F. for two days before being subjected to low temperatures.

The results are shown in Table 2.

It will be seen from Table 2 that the differences between controls at 80°F. and low temperature results increase with the period of exposure more for *A. scutellaris* than for *A. aegypti* and that eggs of the former were more adversely affected by cold than those of the latter. (See statistical note following the summary.)

LARVAE.

All larvae were bred through from eggs deposited in the laboratory and maintained at a constant temperature of 80°F. with an abundant food supply, each separate culture receiving identical treatment as detailed previously by the author (Woodhill, 1936).

One hundred early fourth instar larvae were used in each experiment, and at the conclusion of the experiment were replaced in water at 80°F. with food. A count of dead and living larvae or pupae was made two days after returning them to 80°F.

TABLE 2.
Percentage Hatching of Eggs of A. aegypti and A. scutellaris at Temperatures of 30-40° F.

One hundred eggs in each experiment.

Experiment No.	Temperature.	Time of Exposure.	Percentage Hatched.	
			<i>A. aegypti.</i>	<i>A. scutellaris.</i>
1	40° F.	14 days	12	
2	"	"	16	
3	"	"	57	
4	"	"	25	
5	"	"		0
6	"	"		2
7	"	"		10
8	"	"		1
9	80° F.	"	83	
10	"	"	64	
11	"	"		95
12	"	"		71
13	40° F.	8 days	63	
14	"	"	78	
15	"	"		54
16	"	"		18
17	80° F.	"	90	
18	"	"		47
19	34° F.	3 days	92	
20	"	"		51
21	80° F.	"	51	
22	"	"		71

Table 3 shows the effect of various exposures to temperatures between 37°F. and 46°F. Where two temperatures are given fluctuation took place between the two extremes indicated, but where only one temperature is given the variation was not more than $\pm 1^\circ\text{F}$.

It will be seen from Table 3 that there is a very marked difference between the larvae of the two species in relation to low temperatures, the time factor being of great importance at temperatures between 37°F. and 46°F. From the figures given it will be seen that *A. aegypti* can survive a much longer exposure to cold conditions than *A. scutellaris*, the latter being practically all killed by 48 hours' exposure to temperatures of 40°F. to 46°F., while the former suffer only a small mortality.

The difference between the survival rates of *A. scutellaris* exposed for 18 and 24 hours at 37°F. to 40°F. is also quite striking.

PUPAE.

A number of experiments were also carried out with pupae, which were bred up in the normal way at 80°F. and transferred to 40°F. within twelve hours of pupation. The pupae were then replaced at 80°F. and the percentage survival determined by the number of adults which successfully emerged.

The results are shown in Table 4.

TABLE 3.
Effect of Various Exposures to Temperatures Between 37° and 46° F.

One hundred larvae in each experiment.

No. of Experiment.	Temperature.	Time.	Percentage Alive.	
			<i>A. aegypti</i> .	<i>A. scutellaris</i> .
1	40° F. to 46° F.	24 hours		33
2		" "		52
3		" "	100	
4		" "	92	
5		48 "		4
6		" "		2
7		" "	82	
8		" "	85	
9	40° F.	24 hours		18
10		" "	91	
11		48 "		0
12		" "		0
13		" "	84	
14		" "	100	
15		72 "		0
16		" "	0	
17	37° F. to 40° F	18 hours		79
18		" "		87
19		" "		81
20		" "		81
21		" "	100	
22		" "	98	
23		" "	100	
24		" "	90	
25		24 hours		23
26		" "		28
27		" "		28
28		" "		26
29		" "	93	
30		" "	83	
31		" "	93	
32		" "	91	

TABLE 4.
Effect of Temperature of 40° F. on Pupae within 12 Hours of Pupation.

Variable number of pupae in each experiment.

No. of Experiment.	Temperature.	Time.	No. of Pupae.	Percentage Adults Emerged.	
				<i>A. aegypti</i> .	<i>A. scutellaris</i> .
1	40° F.	24 hours	17	82	
2		" "	30	100	
3		" "	39		61
4		" "	50		50
5		" "	50		26
6		72 hours	50	22	
7		" "	33	15	
8		" "	92	21	
9		" "	68	22	
10		" "	45		0
11		" "	40		0
12		" "	70		0

Table 4 again shows a marked difference between the two species, in the pupal stage, when kept at 40°F. for 72 hours, with no very significant difference for 24 hours. The figures indicate that a complete kill of *A. scutellaris* pupae takes place if exposed for three or more days to 40°F., while a considerable proportion of *A. aegypti* survive.

ADULTS.

A small series of adults of both species were also bred out, kept at 80°F. and 70% to 80% humidity, given raisins as food and one blood meal, and eight days after emergence were transferred to a low temperature chamber. After exposure they were replaced in the warm room and examined after four hours. The results are shown in Table 5.

TABLE 5.
Effect of Exposure of Adults to Low Temperatures.

Temperature.	Time.	No. of ♀♀	No. of ♂♂	Number Alive.			
				<i>A. aegypti</i> .		<i>A. scutellaris</i> .	
				♀	♂	♀	♂
40° F.	24 hours	55	25	54	25		
"	" "	50	23			6	0
"	72 hours	54	25	49	8		
"	" "	6	0			0	0

The survivors of both species after 24 hours at 40° F. were replaced for a further 48 hours, making 72 hours in all with an interval of four hours at 80°F., during the first examination for survivors. Any specimens showing movement after four hours were considered to be alive. The surviving specimens of *A. aegypti* lived for several weeks after the experiment.

It is obvious from Table 5 that the adults of *A. aegypti* are able to survive cold conditions which are fatal to adults of *A. scutellaris*.

SUMMARY.

(1) The experiments indicate that there are very marked physiological differences between *A. aegypti* and *A. scutellaris* in relation to desiccation of the eggs and the ability to withstand cold in the remaining stages, the former species being much more resistant.

(2) Even under optimum conditions of temperature and humidity only a very small percentage of eggs of *A. scutellaris* remain viable after approximately 80 days in the dry state, whereas a large proportion of eggs of *A. aegypti* survive similar conditions.

(3) Under natural conditions of temperature and humidity throughout winter, spring and early summer in the Sydney district all eggs of *A. scutellaris* were killed when allowed to remain dry for approximately 80 days, while a large proportion of eggs of *A. aegypti* hatched.

(4) Eggs of *A. scutellaris* exposed for three days to 34°F. were not significantly affected, but exposure to 40°F. for 14 days killed a significantly larger proportion of the eggs of *A. scutellaris* than of *A. aegypti*.

(5) Larvae of *A. scutellaris* were killed by exposure to 40°F. for 48 hours, while those of *A. aegypti* were not adversely affected.

(6) Pupae of *A. scutellaris* were killed by exposure to 40°F. for 72 hours, while a small proportion of *A. aegypti* survived.

(7) Adults of *A. scutellaris* were all killed by exposure to 40°F. for 72 hours, while a large proportion of *A. aegypti* survived. Females of both species were more resistant to cold than males.

(8) Indications are that *A. scutellaris* is specialized for existence under tropical conditions and would not be likely to establish itself permanently in sub-tropical or temperate zones where *A. aegypti* is commonly found. The present known distribution of the two species agrees with this finding.

(9) Attempts were made to cross male *A. aegypti* with female *A. scutellaris* and vice versa, but although apparent copulation took place and some hundreds of eggs were deposited, none of these proved fertile.

STATISTICAL NOTE.

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All of the conclusions based on the foregoing experimental data require very little further justification, with the possible exception of those concerned with Table 2. The following analysis was thus confined to this table.

First the inverse sine transformation was applied to all of the data to allow a more reasonable application of normal analysis of variance methods. Next the differences between control results and cold temperature results for each species at each time of exposure were obtained. Two weighted linear regression lines showing the dependence of these differences on exposure time were found separately for each of the species. Both lines were forced through the origin: zero difference at zero exposure. The average of two regression coefficients was, as can be expected, highly significant, and the difference between them, which is the most important point of the analysis, gave a *t* based on 4 d.f. of 1.54. Using a one-tail significance test, this is significant at the 10% level.

Analysis of Variance.

	<i>n</i>	<i>S.S.</i>	<i>M.S.</i>
Deviations of differences from zero	6	6,313	1,052
Regression (both lines pooled)	2	5,366	2,683
Mean regression	1	4,805	4,805
<i>Between regressions</i>	1	561	561
Deviations from regression (pooled) ..	4	947	(<i>a</i>) 237
Error	10	1,227	(<i>b</i>) 123

Both of the tests of the regressions were made against the pooled residual mean square for each of the lines. This mean square contains only 4 d.f. and is probably inflated (as can be seen by comparing terms (*a*) and (*b*) in the table) due to small inadequacies in the hypotheses of linear regression; hence the significance of both tests can be considered quite satisfactory.

The significance of the comparisons in this analysis confirms the initial statement above that conclusions based on data in tables other than Table 2 require no further statistical treatment.

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BRYOZOA FROM THE UPPER CARBONIFEROUS OF QUEENSLAND AND
NEW SOUTH WALES.

By JOAN CROCKFORD, M.Sc.
(Twelve Text-figures.)

[Read 27th October, 1948.]

INTRODUCTION.

The bryozoa described in this paper are collections from the Neerkol Series in Queensland and from a thin marine intercalation in the fresh-water Upper Kuttung Series in New South Wales.

The Neerkol Series of Upper Carboniferous age is extensively developed in the Rockhampton district of Queensland, and rocks believed to be of similar age occur at Mt. Barney, near the New South Wales-Queensland border; bryozoa from several localities in each of these areas are described in this paper, and some of the species described are common to both areas. No bryozoa have hitherto been described from the Neerkol Series, although their presence has been recorded by Reid (1930, 36-48) and others. Reid believed that some species of bryozoa from the Neerkol Series were identical with species from the Lake's Creek Quarry, also near Rockhampton. Study of the bryozoa from Lake's Creek Quarry has indicated that these beds are of Lower Permian age (Crockford, 1945, 125), and none of the species from the Neerkol Series described in this paper is identical with any species so far known from Lake's Creek.

In the districts immediately to the north of the Hunter River in New South Wales the Upper Carboniferous includes a thick series of fresh-water glacial and volcanic beds, the Upper Kuttung Series. Recently Dr. G. D. Osborne and a party of students from the University of Sydney found marine fossils on a narrow horizon in the Upper Kuttung Series at Stroud, this horizon being apparently a thin marine intercalation in the fresh-water beds. The marine fossils collected from this horizon include a number of bryozoa, and these species are described in this paper. Two of the species occurring on this horizon in the Upper Kuttung are identical with species occurring both at Mt. Barney and in the Neerkol Series near Rockhampton. From this it appears that the Upper Kuttung Series is at least in part to be correlated with the Neerkol (p. 20).

No specimens of bryozoa were available for study from the Kullatine Series, the marine equivalent of the Upper Kuttung Series in the Manning R. district of New South Wales. Thick marine sediments of Upper Carboniferous age, the Emu Creek Series, are found in the Drake district of New South Wales, and are believed to represent a southern continuation of the Neerkol Series. Voisey (1936) has recorded abundant fenestrate bryozoa from horizons in this series. Material from this series in the collections of the Australian Museum was examined in the hope of finding bryozoans from this series for comparison with those found in the Neerkol, but unfortunately there seem to be no bryozoans amongst the collections.

My thanks are due to Dr. Dorothy Hill, of the University of Queensland for the loan of specimens from the Neerkol Series, and to Dr. G. D. Osborne for the specimens which he collected from the Upper Kuttung, and especially to Professor L. A. Cotton for the help which he has given me in enabling me to complete this paper.

DESCRIPTION OF SPECIES.

Order CYCLOSTOMATA Busk.

Family FISTULIPORIDAE Ulrich.

Sub-Family HEXAGONELLINAE Crockford.

Genus FISTULAMINA Crockford, 1947.

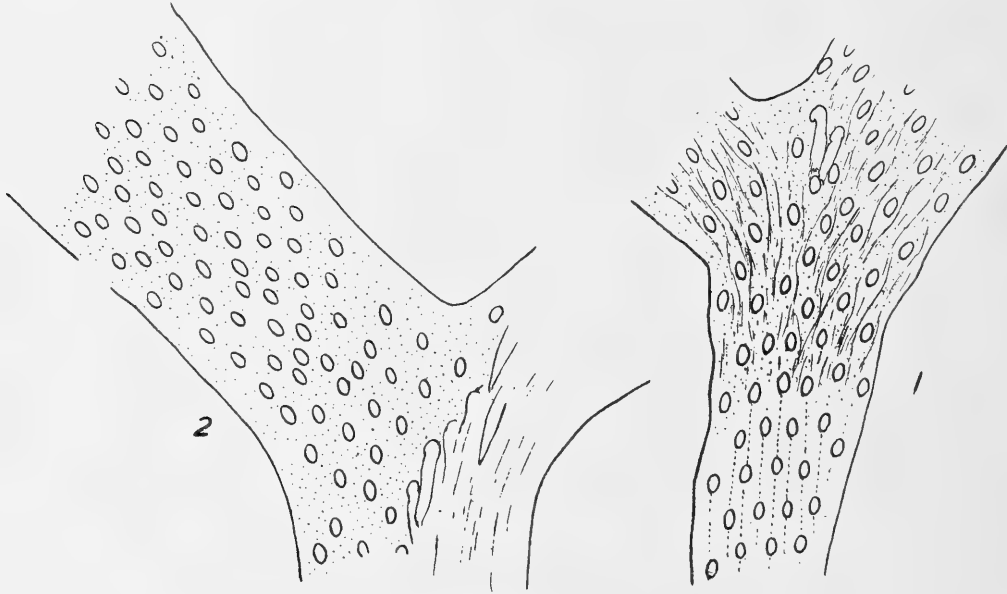
Fistulamina Crockford, 1947, 28.

FISTULAMINA FRONDESCENS, n. sp. (Text-figures 2, 2A).

Holotype: 7427, Sydney Univ. Colln.*Horizon and Locality*: Marine intercalation in the Upper Kuttung Series, Stroud.

Fistulamina with broad, rapidly and rather irregularly bifurcating bifoliate branches; zoecial apertures large, oval, in ten to eleven rows on each surface of the branches, and widely spaced.

The zoarium is bifoliate, consisting of broad, rapidly bifurcating, flattened branches, 3.5 to 4 mm. in width and only about 0.6 mm. in their greatest thickness. The colony reached a considerable size, the holotype being an incomplete specimen more than 7.5 cm. high. On each surface the branches bear normally 10 or 11 rows of large oval zoecial apertures, the number of rows increasing rapidly prior to bifurcation of the



Text-figures 1, 2.

Fig. 1.—*Fistulamina dispersa*, n. sp., weathered surface of the holotype, $\times 7$. The broken line in the lower part of this figure indicates the rows of zoecia.

Fig. 2.—*Fistulamina frondescens*, n. sp., weathered surface of the holotype, $\times 7$.

branch; there is a very narrow non-celluliferous margin along each margin of the branches. Bifurcation of the branches occurs in the plane of the mesial lamina, and successive bifurcations are usually but not always on opposite sides of the main stem. The distance between the bifurcations varies considerably from less than 5 to more than 12 mm. The zoecial apertures are oval, from 0.26 to 0.31 mm. long and 0.19 to 0.22 mm. wide; they are surrounded by thin peristomes, which are highest and most strongly developed on the proximal side of the aperture, the most strongly raised part being deflected slightly towards the closer edge of the branch. No lunaria could be distinguished with certainty, although in some cases the peristome does appear to be

curved to a slightly shorter radius on the raised side. The distance between the centres of successive apertures in the same row is about 0.8 to 1.05 mm., the apertures in the outermost rows being slightly more widely spaced than those in the central rows; in each row there are about 11 apertures in 10 mm. Where it is best preserved the surface between the apertures bears a few broad, shallow ridges and grooves, but these are readily worn away and the surface usually appears smooth.

The internal structure could be seen only on the weathered fracture surfaces of specimens, none of the material being suitable for sectioning. The zooecia are long and tubular, up to about 1.6 mm. in length; for the greater part of this distance they lie flatly along each side of the mesial lamina and then curve upwards to meet the surface very obliquely; occasional tiny vesicles appear to be developed close to the mesial lamina, and the space between the zooecia close to the surface was filled by dense tissue; there are no vertical plates developed between the rows of zooecia, such as those found in *Sulcoretopora*.

This species is a much coarser form than the species of *Fistulamina* previously described from the Burindi Series of New South Wales and the Viséan of Queensland; it is distinguished by its internal structure from species of *Sulcoretopora* of similar size.

FISTULAMINA DISPERSA, n. sp. (Text-figures 1, 1A.)

Holotype: F8928, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, Mt. Barney, Pors. 193-4, Par. Palen (holotype and F8924, Univ. Queensland Colln.); Neerkol Series, ridge above Lion Creek, Stanwell, near Rockhampton (F8913, Univ. Queensland Colln.).

Fistulamina with rather narrow, straplike bifoliate branches; zooecial apertures oval, widely spaced, in seven to nine rows on each surface of the branch; surface between the apertures striated.



Text-figures 1A, 2A.

Fig. 1A.—*Fistulamina dispersa*, n. sp., part of the holotype, $\times 1$.

Fig. 2A.—*Fistulamina frondescens*, n. sp., part of the holotype, $\times 1$.

The zoarium is bifoliate, consisting of narrow straplike branches about 2.6 to 3 mm. in width, which bifurcate at intervals of about 10 mm.; the branches are very thin compared with their width, their greatest thickness being about 0.5 mm. On each surface the branches bear 7 to 9 rows of zooecial apertures, the number of rows increasingly rapidly before bifurcation. The zooecial apertures are long and oval, about

0.26 × 0.17 mm. in diameter, and are surrounded by slight peristomes, which are more strongly raised on the proximal side of the aperture; lunaria do not appear to be developed. There are about nine apertures in 10 mm., the distance between successive apertures in the same row being from 1.0 to 1.2 mm. The surface between the apertures is ornamented by strong and sharp but fine ridges and grooves.

The internal structure is shown only on weathered surfaces of the specimens; the zooecia are long and tubular, up to 1.5 mm. in length; for the greater part of this distance they lie back to back along the mesial lamina, then bend upwards rather sharply to the surface, the curve to the surface being particularly sharp on the lower side close to the mesial lamina. No vertical plates occur between the rows of tubes, but a few small vesicles occur close to the mesial lamina; close to the surface the zooecia were separated by dense tissue, now usually removed by weathering.

The specimens from the ridge above Lion Creek appear identical with those from Mt. Barney except that their apertures are slightly more closely spaced; in their other characters the specimens from these two localities are so similar that they appear to belong to the same species.

Order TREPOSTOMATA Ulrich.

Family BATOSTOMELLIDAE Ulrich.

Genus LEOCLEMA Ulrich, 1882.

Leioclema Ulrich, 1882, 14.

LEIOCLEMA ?, sp. indet.

The only batostomellid noticed in any of the specimens from the Neerkol or Upper Kuttung Series was a single very weathered specimen (on F8914, Univ. Queensland Colln., from ridge above Lion Ck.) of a thin batostomellid with large polygonal zooecia separated by numerous small polygonal mesopores, the abundance of which suggest that it is probably a species of *Leioclema*. It is here recorded to indicate the presence of this family in the Upper Carboniferous of Queensland.

Order CRYPTOSTOMATA Vine.

Family FENESTRELLINIDAE Bassler.

Genus FENESTRELLINA d'Orbigny, 1849.

Fenestrellina d'Orbigny, Bassler, 1935, 111.

FENESTRELLINA MALCHI, n. sp. (Text-fig. 4.).

Holotype: 10 on F8915, Univ. Queensland Colln.

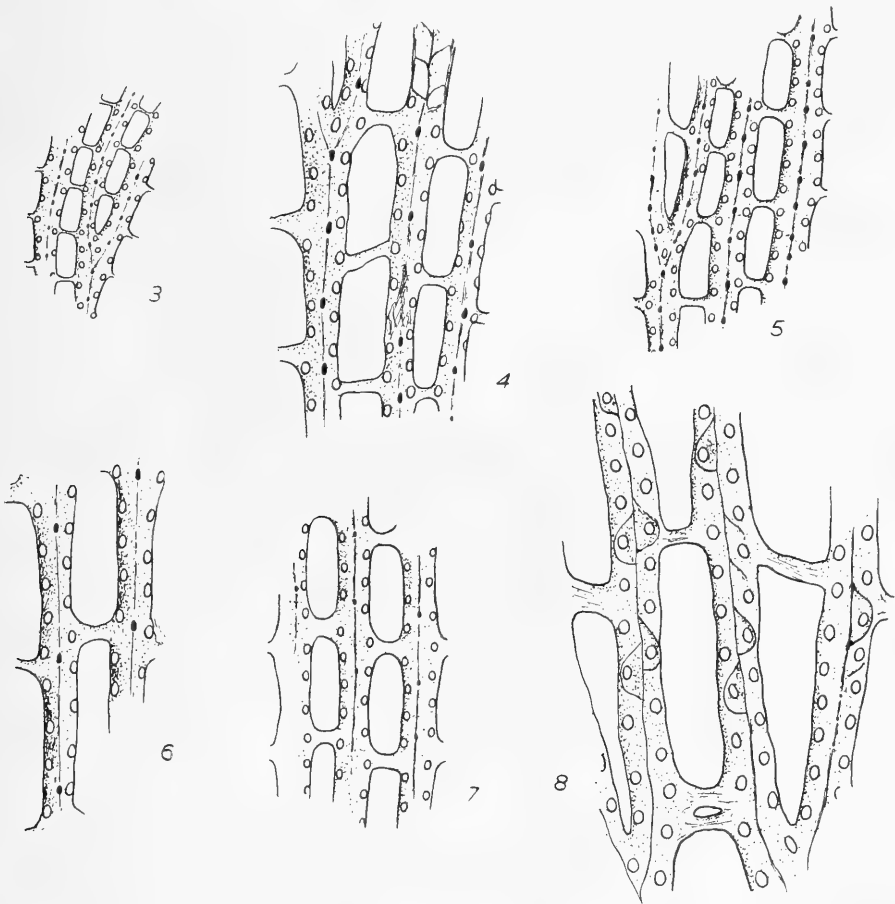
Horizon and Locality: Neerkol Series, Malchi Creek, Rockhampton district (holotype and 11, 11a. on F8915, 18 on F8916, Univ. Queensland Colln.); Neerkol Series, Mt. Barney, Pors. 193-4, Par. Palen (F8923, Univ. Queensland Colln.); Neerkol Series, Mt. Barney, Pors. 127v and 202, Par. Palen (F8932, Univ. Queensland Colln.); Marine intercalation in Upper Kuttung Series, Stroud (7429-32, Univ. Sydney Colln.).

Coarse Fenestrellina, with large rectangular fenestrules; four, sometimes three, zooecia to a fenestrule; carina high but not sharp, nodes large, high, and distant.

The zoarium is coarsely fenestrate, the branches and dissepiments being slender compared with the large rectangular fenestrules. There are 6 to 7 fenestrules in 10 mm., and usually between 14 and 18, but sometimes fewer, branches in the same distance. The branches are comparatively slender, generally between 0.32 and 0.44 mm., but sometimes up to 0.6 mm. in width; they bear two rows of zooecial apertures separated by a high but not sharply defined median carina, which bears a single row of large, high nodes. The nodes are usually elongated along their bases, and are widely spaced, 0.6 to 1.0 mm. apart; about 11 to 14 nodes occur in 10 mm. The zooecial apertures are small and round, 0.16 mm. in diameter; there are 4, rarely 3, apertures to a fenestrule; the distance between the centres of successive apertures is 0.37 to 0.5 mm., and there are about 23 apertures in 10 mm. The fenestrules are rectangular and are between

1.2 and 1.75 mm. in length and from 0.26 to 1.2 mm., but usually between 0.45 and 0.7 mm., in width; the width of the dissepiments is 0.1 to 0.22 mm., rarely to 0.3 mm. The dissepiments are rounded and are depressed below the level of the branches on the obverse surface; on the reverse surface both branches and dissepiments are smooth and evenly rounded. When the reverse surface of the branches is slightly weathered numerous very fine longitudinal striae are shown. The zooecia are rhomboidal to rather oval in outline, and the vestibules are sloping and meet the surface at an angle of about 45° .

There are two species described from Lake's Creek which show a general resemblance to this common Neerkol species, *Fenestrellina sparsa* Crockford and *F. rockhamptonensis* Crockford. This species is distinguished from *F. sparsa* by its rather smaller size and more regular habit of growth, the closer spacing of the nodes and the smaller fenestrules. *F. rockhamptonensis* has much larger nodes, which are rather more widely spaced and are more irregularly arranged than in this species, and it also has more closely spaced zooecial apertures and smaller fenestrules than *F. malchi*.



Text-figures 3-8.

Fig. 3.—*Fenestrellina micropora*, n. sp. Obverse surface of the holotype, $\times 10$.

Fig. 4.—*Fenestrellina malchi*, n. sp. Obverse surface of the holotype, $\times 10$.

Fig. 5.—*Fenestrellina osbornei*, n. sp. Obverse surface of the holotype, $\times 10$.

Fig. 6.—*Fenestrellina* cf. *malchi*. Obverse surface of a specimen (13 on F8915, Univ. Queensland Colln., from Malchi Ck.), which resembles this common Neerkol species except in the spacing of its nodes, which are more widely spaced. $\times 10$.

Fig. 7.—*Fenestrellina rectangularis*, n. sp. Obverse surface of the holotype, $\times 10$.

Fig. 8.—*Fenestrellina cincta*, n. sp. Obverse surface of the holotype, $\times 10$.

FENESTRELLINA OSBORNEI, n. sp. (Text-fig. 5.)

Holotype: On 7430, Univ. Sydney Colln.

Horizon and Locality: Marine intercalation in the fresh-water Upper Kuttung Series, Stroud (holotype and 7433-5, Univ. Sydney Colln.); Neerkol Series, ridge above Lion Creek, Stanwell (F8913-4, Univ. Queensland Colln.); Neerkol Series, Malchi Creek, Rockhampton district (21 on F8916, Univ. Queensland Colln.); Neerkol Series, Por. 2v, Par. Stanwell (F8920, 1, Univ. Queensland Colln.); Neerkol Series, Mt. Barney, Pors. 193-4, Par. Palen (F8926, Univ. Queensland Colln.).

Fine Fenestrellina, meshes fine and regular, three to four zoecial apertures to a fenestrule; carina slight, nodes in a single row, high and closely but rather irregularly spaced.

The zoarium is fenestrate and is fine-meshed, there being about 9 fenestrules and 15 to 18 branches in 10 mm. The branches are thin and straight, 0.28 to 0.39 mm. wide, and rarely bifurcate; they bear two rows of zoecial apertures, increasing to three only immediately before bifurcation. The carina is poorly developed, but there is a single row of high, prominent, spine-like nodes, closely but not very regularly spaced, their distance apart being 0.33 to 0.55 mm.; about 24 of these nodes occur in 10 mm. The zoecial apertures are round, about 0.14 mm. in diameter, and are surrounded by thin, rather high peristomes; there are 3 to 4 apertures in the length of each fenestrule and about 32 in 10 mm., the distance between the centres of successive apertures being 0.28 to 0.35 mm. The fenestrules are oval, 0.8 to 1.07 mm. long and about 0.21 to 0.43 mm. wide; the width of the dissepiments is 0.04 to 0.11 mm., and the length of one fenestrule and one dissepiment from 0.9 to 1.15 mm. The dissepiments are rounded and depressed below the level of the branches on the obverse surface; on the reverse surface both branches and dissepiments are smooth and evenly rounded and they are of about the same thickness. Where the reverse surface has been slightly weathered the backs of the branches are covered by very numerous fine longitudinal striae; the cells are rhomboidal in shape.

This common Neerkol species resembles in its general appearance the two most widespread species of *Fenestrellina* occurring in the Permian of eastern Australia, *F. fossula* (Lonsdale) and *F. dispersa* Crockford. It is, however, a larger species than either of these Permian forms, and differs also in the spacing of its zoecia and particularly in the spacing of the nodes.

FENESTRELLINA MICROPORA, n. sp. (Text-fig. 3.)

Holotype: A/F8913, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, ridge above Lion Creek, Stanwell (holotype and B/F8913, Univ. Queensland Colln.).

Very fine Fenestrellina, with two zoecia to a fenestrule, and with high, sharp, relatively wide-spaced nodes.

The zoarium is very finely fenestrate, there being about 20 fenestrules and 28 branches in 10 mm. The branches are straight, about 0.22 mm. in width, and bifurcate infrequently; they bear two rows of zoecial apertures, with three rows developed only immediately before bifurcation. The zoecial apertures are tiny, 0.09 mm. in diameter, and are surrounded by slight, thin peristomes. There are two apertures in the length of each fenestrule, one of these usually being placed at the end of a dissepiment and the other at the centre of the fenestrule. There are about 42 apertures in 10 mm., the distance between the centres of successive apertures being from 0.21 to 0.26 mm. There is a slight median carina between the two rows of apertures and this bears a single row of small, sharp, evenly spaced nodes; these nodes are placed from 0.28 to 0.32 mm. apart, and there are about 33 nodes in 10 mm. The fenestrules are from 0.45 to 0.55 mm. long and are about 0.17 to 0.22 mm. wide; the width of the dissepiments is 0.04 to 0.06 mm. The dissepiments are rounded and are depressed a little below the level of the branches on the obverse surface.

Numerous specimens of this tiny and distinctive species occur in the mudstones at the type locality of the Neerkol Series; its small size readily differentiates it from other species occurring in this series. Of species described from the Upper Palaeozoic

of Australia this form is most closely comparable with *Fenestrellina horologia* (Brennall), which occurs in the Permian of Western Australia and Queensland. *F. horologia* is, however, a rather coarser species and has more widely spaced zooecial apertures and rather more closely spaced nodes than this form.

FENESTRELLINA CINCTA, n. sp. (Text-fig. 8.)

Holotype: F8919, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, Malchi Creek, Rockhampton district.

Very coarse Fenestrellina, six to ten zooecia to a fenestrule, slight carina with no nodes.

The zoarium is very coarsely fenestrate, there being 8 to 9 branches and about 2.5 fenestrules in 10 mm. The branches are straight and bifurcate rather rapidly; they are normally between 0.5 and 0.61 mm. wide, and bear two rows of zooecial apertures separated by a very slight ridge-like median carina; no nodes appear to have been developed. The zooecial apertures are large, about 0.18 mm. in diameter, and are surrounded by thin, high peristomes; many of the apertures were closed by a centrally perforated calcareous plate. The apertures are placed on the broad, flattened sides of the branches; frequently the zooecial apertures are placed in the centre of an oval depressed area, bordered by a thin and very distinct ridge. There are from 6 to 10 zooecia in a fenestrule, and about 19 in 10 mm., the distance between the centres of successive apertures being from 0.47 to 0.57 mm. The fenestrules are long, narrow, and irregularly shaped; they are normally from 2.2 to 4.6 mm. long, but occasionally a single very short fenestrule is developed; the width of the fenestrules is 0.6 to 1.05 mm., and the width of the dissepiments, which are transversely striate on the obverse surface, is about 0.19 to 0.3 mm. The dissepiments are depressed below the level of the branches on both obverse and reverse surfaces; on the reverse surface both branches and dissepiments are smooth and rounded. The zooecial cells are short, with sloping vestibules which meet the surface at about 45°.

This form resembles *Fenestrellina expansa* Crockford, from the Lower Permian at Lake's Creek, but has a more regular growth form with straight instead of flexuous branches, and has smaller and rather more closely spaced apertures and a slighter carina than *F. expansa*. The surface ridges around the apertures are a very distinctive characteristic of this species.

FENESTRELLINA RECTANGULARIS, n. sp. (Text-fig. 7.)

Holotype: 37 on F8924, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, Mt. Barney, Pors. 193-4, Par. Palen (holotype and 42 on F8927, 43 on F8929, Univ. Queensland Colln.); Neerkol Series, Malchi Creek, Rockhampton (25 on F8917, Univ. Queensland Colln.).

Fenestrellina with three to four zooecia to a fenestrule, nodes small and sharp, rather widely spaced.

The zoarium is fenestrate, with 8 to 9 fenestrules and about 14 branches in 10 mm. The branches are straight and rarely bifurcate; they are from 0.28 to 0.35 mm. in width and bear two rows of zooecial apertures separated by a distinct, sharp-sided, but not high carina, which bears a single row of small, sharp nodes spaced 0.6 to 0.78 mm. apart, there being about 15 of these nodes in 10 mm. The zooecial apertures are small and rounded, 0.1 to 0.15 mm. in diameter, and there are either 3 or more often 4 apertures to a fenestrule, and there are about 28 apertures in 10 mm., the distance between the centres of successive apertures being 0.3 to 0.41 mm. The fenestrules are rectangular, 0.9 to 1.25 mm. long and 0.35 to 0.5 mm. wide; the dissepiments are from 0.07 to 0.17 mm. in width, and the length of one fenestrule and one dissepiment is from 1.02 to 1.4 mm.

This small species, whose rectangular fenestrules and usually rather closely spaced branches give it a very characteristic regularly meshed appearance, is one of the most common species from Pors. 193-4, Par. Palen.

Genus POLYFORA M'Coy, 1844.

Polypora M'Coy, 1844, 207.

POLYFORA PUSTULOSA, n. sp. (Text-fig. 9.)

Holotype: 30/F8920, Univ. Queensland Colln.*Horizon and Locality*: Neerkol Series, Por. 2v, Par. Stanwell.*Fine Polypora, zooecia in three to four rows, with three to four apertures to a fenestrule; apertures pustulose, the surface between them depressed and without nodes.*

The zoarium is fenestrate and has a very regularly meshed appearance; in 10 mm. there are 8 fenestrules and 11 to 12 branches. The branches are slightly rounded on the obverse surface and bear three to four rows of zooecial apertures with two or three rows just after and four or five rows just before bifurcation, which occurs at rather distant intervals. The width of the branches is from 0.47 to 0.6 mm. where there are three and about 0.7 mm. where there are four rows of zooecia. There are 3 to 4 apertures to a fenestrule, the distance between the centres of successive apertures being 0.32 to 0.39 mm.; there are about 27 apertures in 10 mm. The apertures themselves are small and rounded, about 0.09 mm. in diameter; although they are surrounded by only slight, thin peristomes, each aperture is raised above the general surface of the branch so that the apertures are slightly pustulose and the surface between them a little depressed. The fenestrules are oval and regular in appearance; they are from 1.1 to 1.26 mm. long and 0.54 to 0.76 mm. wide, and the width of the dissepiments is from 0.15 to 0.22 mm.; the length of one fenestrule and one dissepiment is from 1.28 to 1.5 mm. On the obverse surface the dissepiments are evenly rounded and are usually depressed slightly below the level of the branches. The reverse surface was not shown. Very occasionally a large spherical surface cell of the type described by Ulrich in some Mississippian fenestellids occurs behind an aperture; Ulrich doubtfully referred to these cells as ovicells and they occur occasionally in many species of Upper Palaeozoic fenestellids.

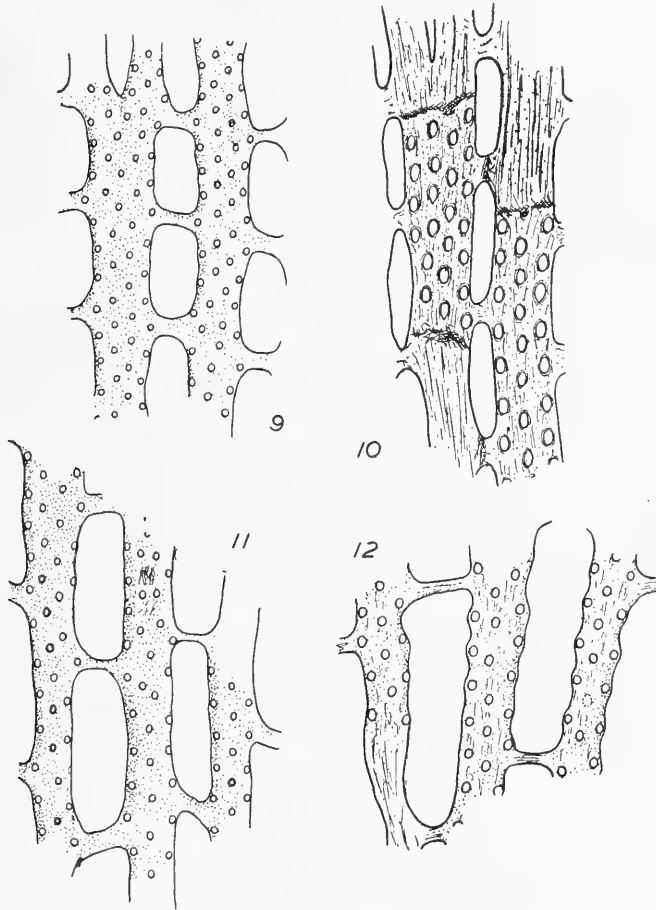
This species is differentiated from *Polypora woodsi* (Etheridge), which occurs in the Permian of New South Wales and Queensland and which it closely resembles in the general size of its zoarium, by having 3 to 4 rows of zooecia instead of regularly only 3 rows, and by the fact that it is the apertures themselves which give the pustulose appearance to the surface in this species, whereas in *P. woodsi* the apertures are depressed, and regular and strongly developed nodes upon the surface between the apertures give a pustulose appearance to the branches; no nodes are developed in this species.

POLYFORA NEERKOLENSIS, sp. nov. (Text-fig. 10.)

Holotype: F8931, Univ. Queensland Colln.*Horizon and Locality*: Neerkol Series, Mt. Barney, Fors. 127v and 202, Par. Palen (holotype); Neerkol Series, Mt. Barney, Fors. 193-4, Par. Palen (F8926, Univ. Queensland Colln.); Neerkol Series, Por. 2v, Par. Stanwell (F8920-2, Univ. Queensland Colln.).*Coarse Polypora, with about six fenestrules in 10 mm.; zooecia in three rows; apertures large, three, sometimes four, to a fenestrule; surface ridged and grooved between the apertures, nodes absent.*

The zoarium is fenestrate and rather coarse meshed, there being 5.5 to 6 fenestrules and 8 to 10, rarely 12, branches in 10 mm. The branches are broad and are flattened on the obverse surface; they bear usually 3 rows of zooecial apertures, with 2 to 3 after and 4 to 5 rows before bifurcation, and sometimes with 4 rows for a long distance before bifurcation. The width of the branches is usually 0.54 to 0.67, rarely to 0.8 mm., where there are three rows of zooecia, and is about 0.45 mm. where there are two rows and 0.7 to 0.87 mm. where there are four rows. The zooecial apertures are large, 0.2 to 0.26 mm. long and 0.15 to 0.2 mm. wide, being oval or when well-preserved rather pyriform in outline; the peristomes are thin and slightly raised. There are 4, rarely 5, apertures in the length of each fenestrule, the distance between the centres of successive apertures being 0.35 to 0.52 mm.; there are about 24 apertures in 10 mm.

Nodes are not developed, the surface between the apertures being faintly pitted and marked by fine faint ridges and grooves. The fenestrules are oval, 1.1 to 1.8 mm. long and 0.24 to 0.87 mm. wide; the dissepiments are 0.17 to 0.4 mm. wide, the length of one fenestrule and one dissepiment being 1.3 to 1.9 mm. The dissepiments are rounded on the obverse surface and are slightly depressed below the level of the branches. On the reverse surface both branches and dissepiments are rounded and are rather coarsely granular, the dissepiments being thinner than the branches; where the outermost layer of the reverse surface is worn away the backs of the branches show numerous fine longitudinal striae; the zoecial cells are oval in outline on the basal plate.



Text-figures 9-12.

- Fig. 9.—*Polypora pustulosa*, n. sp. Obverse surface of the holotype, $\times 10$.
 Fig. 10.—*Polypora neerkolensis*, n. sp. Obverse surface of the holotype, $\times 10$.
 Fig. 11.—*Polypora tenuirama*, n. sp. Obverse surface of the holotype, $\times 10$.
 Fig. 12.—*Polypora palenensis*, n. sp. Obverse surface of the holotype, $\times 10$.

POLYPORA PALENENSIS, n. sp. (Text-fig. 12.)

Holotype: F8932, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, Pors. 127v and 202, Par. Palen (holotype and F8933, Univ. Queensland Colln.).

Very coarse Polypora, with three to four rows of zoecia and six to eight zoecia to a fenestrule; zoecial apertures very small.

The zoarium is coarsely fenestrate, there being about 3 fenestrules and 6 to 8 branches in 10 mm. The branches are straight and bifurcate rather rapidly; they are markedly rounded on the obverse surface and bear 3 to 4 rows of apertures, with 2 or 3 rows after and 5 to 6 rows just before bifurcation. The zoecial apertures are very small for the size of the zoarium, being 0.15 mm. in diameter. There are 6 to 8 apertures to a fenestrule, and about 24 in 10 mm., the distance between the centres of successive apertures being 0.37 to 0.47 mm. The fenestrules are rectangular, about 2.5 to 2.95 mm. long and from 0.65 to 1.0 mm. wide; the dissepiments are slender, 0.15 to 0.28 mm. in width. The dissepiments and branches are smooth and finely granular on the reverse surface, both being rather flattened.

POLYPORA TENUIRAMA, n. sp. (Text-fig. 11.)

Holotype: 15 on F8915, Univ. Queensland Colln.

Horizon and Locality: Neerkol Series, Malchi Creek, Rockhampton district (holotype and 12 on F8915, Univ. Queensland Colln.).

Coarse Polypora, with thin branches and dissepiments; zoecia in three to four rows on the branches, four to five apertures to a fenestrule; apertures slightly pustulose, stellate where well preserved.

The zoarium is coarsely fenestrate, the branches and dissepiments being slender for the number of rows of zoecia and the length of the fenestrules. In 10 mm. there are about 11 branches and 4.5 fenestrules. The branches are slightly rounded on the obverse surface and usually bear either 3 or 4 rows of zoecia, with two to three rows just after and either four or five rows just before bifurcation; the width of the branches is about 0.28 to 0.34 mm. where there are two rows of zoecia, increasing to 0.37 to 0.55 mm. where there are three and about 0.62 mm. where there are four rows. There are 4 to 5 zoecial apertures to a fenestrule and about 23 in 10 mm., the distance between the centres of successive apertures being 0.37 to 0.5 mm. The zoecial apertures are small, about 0.12 mm. in diameter; they are slightly pustulose, and when perfectly preserved they are surrounded by thin distinct peristomes and are stellate, about nine tiny radiating spines surrounding each aperture. No nodes appear to have been developed; the surface between the apertures is when well preserved ornamented by very fine longitudinal striae. The fenestrules are rectangular and are from 1.62 to 2.2 mm. long, being usually more than 1.85 mm. long, and they are from 0.32 to 0.76 mm. wide; the dissepiments are thin, 0.11 to 0.26 mm. in width, and are evenly rounded and slightly depressed below the level of the branches on the obverse surface. On the reverse surface both branches and dissepiments are smooth and rounded and they are of about the same thickness. The zoecial cells are oval in outline on the basal plate.

Family ACANTHOCLADIIDAE Zittel.

Genus PENNIRETEPORA d'Orbigny, 1849.

Penniretepora d'Orbigny, Bassler, 1935, 165.

PENNIRETEPORA, spp. indet.

Small fragments of *Penniretepora* occur in specimens from two localities in the Neerkol Series, from Malchi Creek in the Rockhampton district, and from Por. 2v. Par. Stanwell, also near Rockhampton. Although these fragments are too poorly preserved for any description, they are of interest in indicating the presence of this genus in the fauna.

DISTRIBUTION OF THE BRYOZOAN FAUNA.

The relative positions of the horizons within the Neerkol Series from which the Bryozoa described in this paper were collected is not known, and consideration of the distribution of the species here described unfortunately does not suggest any definite correlations between these different localities within the Neerkol Series. Their distribution is, however, significant in indicating that the two localities at Mt. Barney

are definitely of Neerkol age, and also in showing that the Neerkol Series is at least in part coeval with the top part of the Upper Kuttung Series. The Upper Kuttung and Kullatine Series in New South Wales contain abundant evidences of glacial activity, and tillites and varve-shales are of frequent occurrence within these series. Direct evidences of glacial activity are not known to occur in the Neerkol Series, and because of this it has at times been doubted whether the Neerkol is equivalent to any part of the Upper Kuttung. Bryozoa here described from Stroud were collected from an horizon within the main glacial zone at the top of the Upper Kuttung Series, this horizon being some 2,000 ft. below the top of the series; the fact that two of the species of Bryozoa occurring on this horizon at Stroud occur also in the Neerkol Series, both in the Rockhampton district and at Mt. Barney, indicates that at least a part of the Neerkol should be correlated with the Upper Kuttung.

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STUDIES ON FORMIC HYDROGENLYASE IN WASHED SUSPENSIONS OF ESCHERICHIA COLI.

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(Four Text-figures.)

[Read 24th November, 1948.]

INTRODUCTION.

That *E. coli* and certain other bacteria decompose formate with production of molecular hydrogen and carbon dioxide has been known for some time. Studies up till 1937 on the enzyme systems concerned with this and related reactions have been fully reviewed by Stephenson (1937).

In studies on formic hydrogenlyase, attention has been focussed upon the adaptive nature of the system; the presence of formate or fermentable carbohydrate has been found necessary for the production of the enzyme system. According to observations by Waring and Werkman (1944) iron is an essential factor in the growth medium, in order to obtain suspensions with formic hydrogenlyase activity. These workers grew *Aerobacter indologenes* under conditions of continuous aeration in a basal medium containing glucose and inorganic salts. Under these conditions, suspensions with good formic hydrogenlyase activity were obtained, providing the medium contained a sufficient quantity of inorganic iron.

There has been controversy as to whether formic hydrogenlyase activity is due to a single enzyme or to the action of formic dehydrogenase and hydrogenase acting in conjunction. (Stephenson, 1937, Ordal and Halvorsen, 1939, Waring and Werkman, 1944.)

The present studies were undertaken to investigate the relative instability of formic hydrogenlyase in washed suspensions of *E. coli* on keeping and on dilution.

METHODS.

The strain of *E. coli* used in these studies was that described in a previous paper (Lascelles and Still, 1946). It was maintained on nutrient agar. The organisms for experiments were grown on a nutrient broth of the following constitution: 1% glucose, 0.5% peptone (Parke Davis), 0.5% NaCl and 0.1% meat extract ("Globex"). The pH was adjusted to 7.8 before autoclaving. After autoclaving the pH was 7.4. For the preparation of washed suspensions, 5 ml. of a 20-hour culture in the above medium were sown into 1 litre volumes of the broth in 2-litre flasks, and the cultures were incubated for 18 hours at 38°C. The cells were centrifuged, washed once with 50 ml. distilled water and the final suspensions were made up in distilled water; the dry weight of the suspensions varied from 5 to 9 mg./ml.

Formic hydrogenlyase activity was determined in Warburg manometers in an atmosphere of nitrogen, purified by passing over copper coils heated to about 450°C. So that evolution of molecular hydrogen only, was measured, 0.2 ml. 20% KOH and a roll of filter paper were present in the centre well of each Warburg vessel, to absorb the carbon dioxide. Usually additions other than formate were made to the main compartment of the vessel so that they were in contact with the cells during the equilibration period (10 minutes) prior to the addition of formate from the side arm. Formic hydrogenlyase activity was usually determined at pH 6.9, which was found to

* This work was done while the writer was a Linnean Macleay Fellow of the Society in Biochemistry, at the University of Sydney.

be within the optimum range under our conditions. This is in agreement with the results of Stephenson and Strickland (1932). The final concentration of formate was M/30, well within the optimum range of concentration. All experiments were conducted at 38°C.

The sodium formate, adenylic acid and glutathione used in these experiments were manufactured by B.D.H. Wherever possible, all other reagents were B.D.H. Analar grade.

Many results have been expressed as Q_{H_2} , i.e., μ ls. hydrogen evolved from formate/mg. dry weight cells/hour, in an atmosphere of nitrogen. Since the course of hydrogen production was not always linear, the period from which figures for Q_{H_2} were taken has been stated in each table.

RESULTS.

Stability of Suspensions.—Washed suspensions showed marked losses in formic hydrogenlyase activity on standing at room temperature. This loss was not so marked if the suspensions were kept in a refrigerator at 4°C. The degree of loss was conditioned somewhat by the concentration of the suspension. Weak suspensions showed much greater losses than strong suspensions (more than 6.0 mg./ml.).

To illustrate this, the following experiment was set up: A freshly harvested suspension was divided equally into two parts, A and B. A was kept undiluted for 16 hours at 4°C. in air; B was diluted by the addition of an equal volume of distilled water, and

TABLE 1.

Effect of Keeping Suspensions at Different Concentrations.

Each Warburg vessel contained suspension, and 1.5 ml. M/5 phosphate buffer pH 6.9. The side arm contained 0.1 ml. M/1 formate. Distilled water was added to make a final volume of 3.0 ml. 0.2 ml. 20% KOH was in the centre well.

Suspension.	Dry Weight.	Q_{H_2} (0 to 60 Minutes).
0.5 ml. fresh suspension	3.9 mg.	60
0.5 ml. suspension A	3.9 mg.	35
0.5 ml. suspension B	3.9 mg.	8.5

stored under the same conditions as A. The formic hydrogenlyase activity of each suspension was then determined, using the same quantity of cells from each suspension.

Storage of the suspensions in nitrogen or hydrogen did not prevent this loss in activity.

TABLE 2.

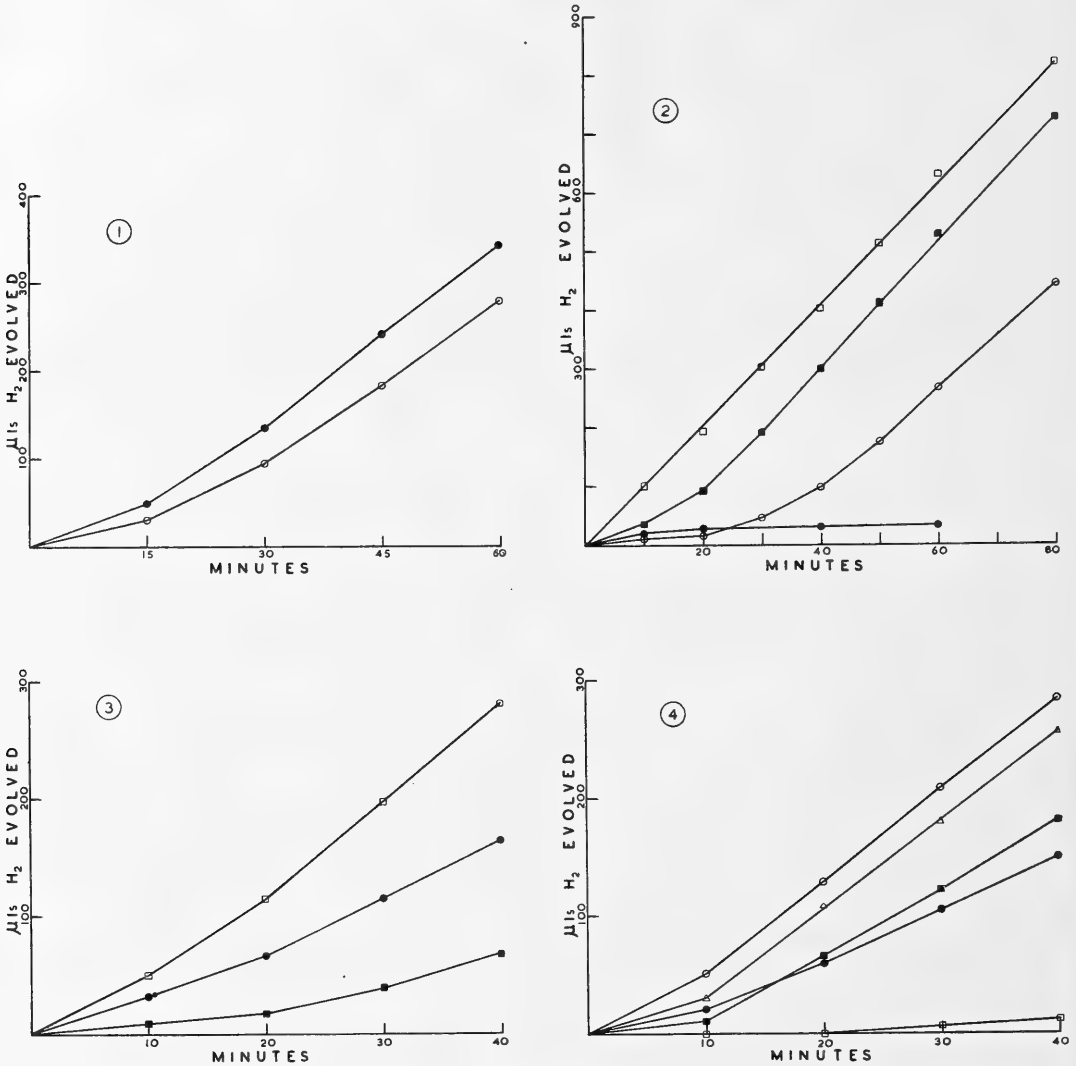
*Effect of Dilution.**

Volume of Suspension.	Dry Weight.	H ₂ Output in 20 Minutes.	Q_{H_2} (0-20 Minutes).
1.0 ml.	7.8 m.g	203 μ l.	78
0.5 "	3.9 "	72 "	55
0.25 "	2.0 "	0 "	0

* Contents of vessels as before.

For many types of experiments it was found that suspensions which had been kept for 18 hours or more at 4°C. were more suitable than fresh suspensions. Particularly did this apply to studies on the stimulatory effects of certain compounds.

Dilution of Suspensions.—Large losses in formic hydrogenlyase activity were noted on dilution of the suspensions, as shown in Table 2.



Text-figures 1-4.

Fig. 1.—Effect of boiled suspension. Contents of vessels as usual. 0.3 ml. suspension (= 2.0 mg. dry wt.) was in each vessel. The suspension had been kept for 18 hours at 4°C. before use.

○—○ Hydrogen output with M/30 formate, in the absence of boiled cells.

●—● Hydrogen output with M/30 formate, in the presence of 1.0 ml. boiled suspension.

Fig. 2.—Course of hydrogen evolution from formate in the presence and absence of glucose. Contents of vessels as usual. 0.3 ml. suspension (= 2.9 mg. dry wt.) was in each cup. The suspension had been kept for 24 hours at 4°C. before use.

●—● Course of hydrogen evolution from M/1,000 glucose, added to the suspension at zero.

○—○ Course of hydrogen evolution from M/30 formate.

□—□ Course of hydrogen evolution from M/30 formate, in the presence of M/1,000 glucose, the glucose being equilibrated with the cells prior to the addition of formate.

■—■ Course of hydrogen evolution from M/30 formate, in the presence of M/1,000 glucose, the glucose being added to the cells simultaneously with the formate.

Fig. 3.—Effect of incubation in air and nitrogen. Contents of vessels as usual. 0.3 ml. suspension (= 2.0 mg. dry wt.) was in each vessel. The cells were freshly harvested.

□—□ Course of hydrogen evolution from M/30 formate with untreated suspension.

●—● Course of hydrogen evolution from M/30 formate with suspension which had been shaken for 140 minutes in nitrogen at 38°C.

■—■ Course of hydrogen evolution from M/30 formate with cells which had been shaken for 140 minutes in air at 38°C.

Addition of boiled suspensions to these diluted suspensions of *E. coli* did result in some restoration of lost activity. This stimulation was more marked with aged suspensions. The supernatant fluid from boiled cells was as active as the whole boiled suspensions. See Text-figure 1.

Further attempts were made to find other agents which could restore this lost activity.

Effect of Additions to Suspensions.—A number of factors were found to stimulate formic hydrogenlyase, but in no case except with high concentrations of adenylic acid was the degree of stimulation as great as with glucose and related fermentable compounds.

In these studies it was usual to use weak suspensions varying in dry weight between 2 and 4 mg./Warburg vessel. In all cases, the compounds investigated were equilibrated with the cells for ten minutes prior to the addition of formate from the side arm.

TABLE 3.
Sugars and Glycolytic Breakdown Products in Relation to Formic Hydrogenlyase Activity of Washed Suspensions.

Compound.	Stimulation of Formic Hydrogenlyase Activity.	Fermentation with Evolution of H ₂ by these Suspensions.
Glucose	+	+
Fructose	+	+
Mannose	+	+
Galactose	Some stimulation after about 90 minutes.	H ₂ evolution after lag of 90 minutes.
Lactose	Do.	Do.
Maltose	Slight stimulation.	Slight.
Sucrose	—	—
Glucose-I-PO ₄	+	+
Hexose diphosphate	—	Slight.
Na gluconate	+	+
Na glycerate	—	—
Na glycerophosphate	—	—
Ethyl alcohol	—	—
Glycerol	—	—
Na acetate	—	—
Na lactate	—	—

+ denotes stimulation of formic hydrogenlyase, or fermentation.
— denotes no stimulation, or no fermentation.

Sugars.—Small amounts of fermentable sugars and certain breakdown products caused marked stimulation of the formic hydrogenlyase of these washed suspensions of *E. coli*. The effect was most marked with suspensions which had a lag period in the course of hydrogen evolution from formate. Hence, aged or diluted suspensions showed the highest degree of stimulation. The active sugars either greatly diminished or eliminated this lag.

Fig. 4.—Reactivation of suspension after incubation in oxygen. Contents of vessels as usual. 0.4 ml. suspension (= 2.4 mg. dry wt.) was in each vessel. Cells had been kept as paste for 24 hours at 4°C.

- Course of hydrogen evolution from M/30 formate with untreated suspension.
- Course of hydrogen evolution from M/30 formate with suspension after shaking in oxygen for 35 minutes at 38°C.
- Course of hydrogen evolution from M/30 formate, in the presence of M/1,000 glucose, with suspension after shaking in oxygen as above.
- Course of hydrogen evolution from M/30 formate, with suspension shaken in oxygen as above, and then with nitrogen for further 35 minutes.
- △—△ Course of hydrogen evolution from M/30 formate, in the presence of M/1,000 glucose, with suspension shaken in oxygen and then in nitrogen as above.

The final concentration of the sugars used in these experiments was M/1,000; control experiments showed that evolution of hydrogen from fermentation of the sugars at this low concentration was very small and could not account for the increases in the rate of hydrogen output in the presence of formate.

Table 3 lists the sugars and glycolytic breakdown products which were studied in relation to formic hydrogenlyase activity of these washed suspensions. The activity of these suspensions with respect to fermentation of these compounds with production of molecular hydrogen is also listed.

For the experiments with formic hydrogenlyase, 2 to 3 mg. dry wt. of cells were used in each vessel. The compound, in final concentration of M/1,000, was equilibrated with the cells prior to the addition of formate from the side arm.

In the fermentation experiments, 6 to 8 mg. dry wt. of cells were used in each vessel. The substrate in final concentration of M/50 was added from the side arm at zero. The atmosphere was N₂. Hydrogen evolution only was measured, CO₂ being absorbed by KOH in the centre well.

Neither did Na glycerate, Na glycerophosphate, ethyl alcohol, glycerol nor Na acetate stimulate at a final concentration of M/150.

It appears that those compounds which were fermented by the cells with evolution of molecular hydrogen caused stimulation in the rate of hydrogen output from formate.

Stimulation by glucose was studied in some detail. Text-figure 2 illustrates the course of hydrogen evolution from formate in the presence and absence of M/1,000 glucose. It is seen that the evolution was linear if the cells had been equilibrated in the presence of glucose prior to the addition of formate from the side arm. Addition of glucose to the suspensions simultaneously with the formate resulted in stimulation of formic hydrogenlyase after an initial lag.

Text-figure 2 also shows that the hydrogen evolution from M/1,000 glucose in the absence of formate was very slight. This was always observed. No corrections were made to the figures recorded, for the evolution of hydrogen observed with glucose alone.

The loss in activity observed as suspensions aged, could be restored to a large extent by the addition of M/1,000 glucose, as shown in Table 4.

Incubation of the cells with M/1,000 glucose for varying periods up to 60 minutes before addition of formate from the side arm resulted in little variation in the degree of stimulation of hydrogen output by the glucose when formate was added.

Organic Coenzymes.—These compounds were studied for their action on formic hydrogenlyase under the conditions described for glucose.

A preparation of flavine adenine dinucleotide made from baker's yeast by the method of Warburg and Christian (1938) was found to be stimulatory. Adenylic acid was very active in a final concentration of not less than M/400; the high concentration necessary suggests that its stimulatory action may have been due to an impurity in the preparation.

When glucose and adenylic acid together were equilibrated with the suspensions prior to addition of formate, the stimulation of formic hydrogenlyase activity was never greater than that obtained with glucose alone.

Glutathione, diphosphopyridine nucleotide (prepared from baker's yeast by the method of Williamson and Green, 1940) and riboflavine (Roche) did not cause any stimulation under these conditions. The only sample of adenosinetriphosphate available caused inhibition.

Inorganic Ions.—Of the inorganic ions studied, phosphate was the most important for formic hydrogenlyase activity.

The activity of the system in borate buffers was much less than the activity in phosphate buffers of the same pH. In these experiments, a check on the final pH was always performed as the alkalinity of borate buffers increased more markedly as the

TABLE 4.
*Effect of Glucose on Suspensions after Storage.**

Age of Suspension.	Volume of Suspension in Each Vessel.	Glucose Concentration.	Q _{H₂} .			
			0-20'	20'-40'	40'-60'	
Freshly harvested suspension ..	0.3 ml.	0	150	340	416	
" " " " " " " " " " " "	0.3 "	M/1,000	378	355	322†	
24 hours' storage‡ ..	0.3 "	0	27	169	277	
" " " " " " " " " " " "	0.3 "	M/1,000	285	299	315	
" " " " " " " " " " " "	0.3 "	M/3,000	199	286	322	
96 hours' storage‡ ..	0.5 "	0	0	0	5	82
" " " " " " " " " " " "	0.5 "	M/1,000	53	76	97	131

* Contents of vessels as before. Suspension dry wt. = 9.6 mg./ml.

† The supply of formate was almost depleted at this stage.

‡ Suspension was stored in the refrigerator at 4° C. and at a concentration of 9.6 mg./ml. dry weight.

formate was decomposed than was observed with phosphate buffers. Addition of phosphate to borate buffers caused increases in formic hydrogenlyase activity, as shown in Table 5.

TABLE 5.
*Effect of Phosphate and Borate Buffers.**

Buffer.	Initial pH.	Final pH.	Additions.	Q _{H₂} .	
				0-20'	20'-40'
M/20 borate ..	6.9	7.8	Nil	40	68
" " " " " " " " " " " "	6.9	7.8	M/150, PO ₄ , pH 6.9	68	113
M/10 phosphate ..	6.9	6.9	Nil	238	258

* Contents of vessels as usual except that in some cases borate instead of phosphate buffer was used. 2.3 mg. dry wt. of cells was used in each vessel; the cells had been stored as a paste for 18 hours at 4° C.

Since it appeared that phosphorylation was involved in some way in the action of formic hydrogenlyase, attempts were made to detect disappearance of inorganic phosphate in the presence of formate, adenylic acid and glucose (cf. Lipmann, 1946). However, no significant results were obtained.

As shown by Stephenson and Stickland (1932), sodium fluoride was strongly inhibitory. M/50 NaF inhibited the formic hydrogenlyase activity by about 70%, this inhibition not being reversed by M/50 magnesium chloride. M/25 NaF inhibited the system from 95-100%.

M/300 ferrous ammonium citrate did not cause any change in the rate of hydrogen evolution from formate. Slight stimulation was observed in the presence of M/300 manganous sulphate.

M/300 magnesium chloride did not have any effect on formic hydrogenlyase activity, but the presence of magnesium ions did result in some increase in the degree of stimulation of the system by adenylic acid.

Incubation of Washed Suspensions.—Incubation of these washed suspensions under various conditions had marked effects on their formic hydrogenlyase activity.

Preliminary incubation at 38°C. of the cells in air or oxygen for 30 minutes or more had a strong inhibitory action on this system. Incubation in nitrogen or hydrogen for the same length of time did not have any great effect on their formic hydrogenlyase activity. If shaken for longer than 60 minutes in nitrogen or hydrogen at 38°C. some losses in activity were observed. See Text-figure 3.

Suspensions which had been inactivated by shaking in air or oxygen could be reactivated in some degree by further incubation in nitrogen or hydrogen, or by the addition of M/1,000 glucose. Nitrogen was as effective as hydrogen in the reactivation.

Text-figure 4 shows that suspensions inactivated by incubation in oxygen were almost completely reactivated by the addition of M/1,000 glucose to the cells after they had been reincubated for 30 minutes in nitrogen. Neither reincubation in nitrogen nor the addition of M/1,000 glucose alone brought about such complete reactivation. The initial rate of hydrogen evolution from formate by cells which had been reactivated by M/1,000 glucose or by reincubation in nitrogen after incubation in oxygen, was identical; however, the rate in the 20–40 minute period was greater with the cells in the presence of glucose.

Some reactivation of the formic hydrogenlyase system, after incubation in oxygen, was obtained by the addition of boiled cells or M/170 adenylic acid, under the conditions described for glucose. However, the effects were not as marked as those obtained with glucose. M/300 succinate and M/150 DL-alanine were ineffective.

Attempts were made to determine whether the activating factors in boiled suspensions could be removed by incubation of the cells for 3–5 hours with buffer (M/10 phosphate, pH 6.9) in oxygen prior to boiling them. However, no significant differences were detected in the action of cells treated thus prior to boiling, and in normal boiled suspensions.

Incubation in Nitrogen with Glucose and Formate: Preliminary incubation of the cells in nitrogen in the presence of buffer, glucose and formate gave suspensions with greatly increased formic hydrogenlyase activity.

The following procedure was adopted: Warburg vessels were set up containing 1.0 ml. fresh suspension, and 1.5 ml. M/5 phosphate buffer, pH 6.9. The side arm contained 0.3 ml. M/10 formate and/or 0.3 ml. M/10 glucose. Final volume was 3.0 ml. 20% KOH was in the centre wells as usual. After filling with nitrogen, the manometers were equilibrated on the bath for 10 minutes, and at zero the contents of the side arms were tipped. Shaking was continued for 90 minutes, hydrogen evolution from formate and glucose having ceased within that time. 2.5 ml. aliquots were removed from each cup, and the cells were spun off; after washing with 10 mls. of distilled water, they were re-suspended in 1.0 ml. distilled water. The formic hydrogenlyase activity was determined as usual on aliquots of these re-suspended cells.

Table 6 records the results of one of these experiments.

Thus preliminary incubation of cells with M/100 glucose increased their formic hydrogenlyase activity when tested after removal of the glucose. Incubation with M/1,000 glucose or M/100 formate for the same length of time did not result in increased activity, but preliminary incubation with both M/100 glucose and M/100 formate resulted in suspensions with greater formic hydrogenlyase activity than those obtained after incubation with glucose alone.

Control experiments showed that cells which had been pre-incubated with M/100 glucose did not evolve molecular hydrogen in the absence of formate.

The formic hydrogenlyase activity of cells pre-incubated with M/100 glucose as above, was no longer stimulated by M/1,000 glucose, whereas that of control suspensions obtained from cells pre-incubated with or without M/100 formate showed the usual

marked stimulation by M/1,000 glucose. Also, glucose-treated suspensions did not show the lag in the evolution of hydrogen from formate; this lag was evident with the suspensions pre-incubated without glucose.

TABLE 6.
Effect of Preliminary Incubation of Cells in Nitrogen with Formate and Glucose.

The re-suspended cells were obtained as above. Dry wt. of suspension as used in the preliminary incubation = 7.9 mg./Warburg vessel. 0.7 ml. (= 4.6 mg.) aliquots from each of the treated suspensions was used in the determination of formic hydrogenlyase activity. Q_{H_2} of suspension before preliminary incubation = 63 (0-30 minutes).

Suspension Incubated Initially with :	Q_{H_2} , After Treatment. 0-30 Minutes.
No addition	60
M/100 formate	61
M/100 glucose	125
M/100 formate and M/100 glucose ..	192

DISCUSSION.

The most noteworthy result obtained from these experiments is the marked stimulation of formic hydrogenlyase by glucose and other fermentable sugars. Sevag, Henry and Richardson (1945) have observed that hydrogen production from formate by suspensions of *E. coli* is greatly increased by the addition of 0.05% yeast extract. This may have been due to the presence of glucose in the yeast extract; also, it is probable that other organic coenzymes are involved in formic hydrogenlyase activity.

Reference to Text-figure 2 shows that M/1,000 glucose did not appreciably alter the final rate of hydrogen evolution from formate, but was effective in eliminating the lag observed in the rate on first adding formate to the suspensions.

It is difficult at present to say whether the results have any bearing on adaptation. Aged suspensions of *E. coli* under the conditions described lost their activity to decompose formate into hydrogen and CO_2 . However, after a relatively prolonged lag period in the presence of formate, formic hydrogenlyase activity appeared again. This lag period was very much shortened by the presence of M/1,000 glucose.

This phenomenon may be related to the studies on adaptation of yeast cells to fermentation of galactose and maltose (Spiegelman, Reiner and Cohnberg, 1947). These workers have investigated the sources of energy for enzymatic adaptation. They observed that, anaerobically, only those exogenous substrates capable of being fermented by the yeast cells were active in stimulating adaptation. Similarly, in our suspensions of *E. coli*, stimulation of formic hydrogenlyase by sugars and derivatives was confined only to those compounds fermented by the cells.

Under our conditions, a lag period in the course of hydrogen output from formate could be induced by first incubating the cells in air or oxygen. Reincubation of the cells in nitrogen followed by the determination of formic hydrogenlyase in the presence of M/1,000 glucose, almost completely restored the lost activity. It is possible that glucose may replace endogenous substrates removed by oxidation during the preliminary aerobic incubation. Stephenson and Stickland (1932) did not observe marked loss of formic hydrogenlyase activity on aeration of their suspensions for 45 minutes at 20°C. However, their conditions were not as drastic as those described in this paper.

Preliminary anaerobic incubation of the cells with glucose resulted in suspensions which attacked formate at a much greater rate. The formic hydrogenlyase of such activated suspensions was not further stimulated by addition of M/1,000 glucose. This again suggests that glucose fermentation provides a factor essential for formic hydrogenlyase activity.

The fact that phosphate appeared to be necessary for formic hydrogenlyase activity may be linked with the formation by fermentation of this factor.

SUMMARY.

Investigation of the formic hydrogenlyase activity in washed suspensions of *E. coli* has shown that marked losses in activity occur when the suspensions are diluted or kept for any length of time. These losses could be largely restored by the addition of glucose or other fermentable sugars and derivatives. Certain other factors were found to be stimulatory to a smaller extent.

Preliminary incubation of these suspensions in air or oxygen resulted in much loss of formic hydrogenlyase activity. Addition of small amounts of glucose or reincubation in nitrogen restored some of this lost activity.

Preliminary anaerobic incubation of the washed cells with glucose gave, after removal of the glucose, suspensions with greatly increased formic hydrogenlyase activity. This activity was not further increased by the addition of small amounts of glucose.

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STUDIES IN THE METABOLISM OF APPLES.

VII. A STUDY OF THE POLYPHENOLASE SYSTEM IN APPLES.

By FRANCES M. V. HACKNEY, M.Sc.*

(Ten Text-figures.)

[Read 24th November, 1948.]

INTRODUCTION.

In recent years several investigators have directed attention to the possible importance of the polyphenolase system in plant respiration. In the literature, polyphenolase is also known as polyphenol oxidase, catechol oxidase, catecholase and tyrosinase. The findings of Boswell and Whiting (1938) and of Baker and Nelson (1943) indicate that the greater part, if not the whole, of the respiration of sliced potato tissue is dependent on the polyphenolase system.

In the enzymic oxidation of catechol by polyphenolase two atoms of atmospheric oxygen are taken up for every molecule of catechol oxidized. The first atom of oxygen is probably utilized in the oxidation of catechol to orthobenzoquinone, and the second atom is thought to be taken up during the further oxidation of the benzoquinone (Nelson and Dawson, 1944). In addition to catalysing the oxidation of ortho-dihydric phenols, polyphenolase is probably capable of catalysing the oxidation of monohydric phenols. The first step in this latter oxidation is probably the conversion of the monohydric phenol to the corresponding *o*-dihydroxy phenol.

Little is known of the mechanism by which polyphenolase is capable of entry into the path of hydrogen transfer in respiration. Robinson and Nelson (1944) consider that in potato tubers the reversible system "dihydroxy phenol-ortho-quinone" may operate adjacent to the terminal oxidase, polyphenolase, in transferring hydrogen from the preceding part of the respiratory chain to molecular oxygen. The darkening of potato tubers, when exposed to air, is attributed by these writers to interference with the system necessary for keeping the hydrogen carrier in the reduced form. Boswell (1945) considers that the respiration of potato tubers depends on two different oxidation systems, the one responsible for the greater part of the activity being the polyphenolase system. Boswell considers also that the polyphenolase system has additional importance as a link between respiration and nitrogen metabolism in potato slices.

Much of the literature on the subject of polyphenolase has been reviewed by Nelson and Dawson (1944). This review need not be repeated here.

The work of Hibbert (1942) was not discussed by Nelson and Dawson. Hibbert pointed out a marked similarity between a phenolic C_6C_3 system related to lignin progenitors and the system of C_4 aliphatic dicarboxylic acids in the Szent-Györgyi cycle (1934, 1935, 1936). The former system differs from the latter in that each of its members contains a guaicyl or syringyl group and a carbinol group in place of the two carboxyl groups present in members of the latter group. The two systems are compared with each other below:

* Most of the investigations described in this paper were carried out while the writer held a Linnean Macleay Fellowship in Plant Physiology.

Szent-G. C ₄ System (Animal). R' represents COOH.	Hibbert C ₆ C ₃ System (Plant). R represents guaicyl or syringyl.
(A) R'.CH ₂ .CO.R' -2H ↑↓ +2H	(A') R.CH ₂ .CO.CH ₂ OH -2H ↑↓ +2H
(B) R'.CH ₂ .CHOH.R' ↓ -H ₂ O	(B') R.CH ₂ .CHOH.CH ₂ OH ↓ -H ₂ O
(C) R'.CH=CH.R' fumaric -2H ↑↓ +2H	(C') R.CH=CH.CH ₂ OH coniferyl/alcohol -2H ↑↓ +2H analogue of fumaric
(D) R'.CH ₂ .CH ₂ .R' succinic acid.	(D') R.CH ₂ .CH ₂ .CH ₂ OH

According to Hibbert the isomeric form of A', R.COCH₂.CH₂OH, may have a similar function to A', while the interconvertible reduction products of B' and its isomer (R.CHOH.CH₂.CH₂OH, R.CH₂.CHOH.CH₂OH) might provide analogues of Krebs' citric and isocitric acids (see Krebs, 1943).

Hibbert's work was the first to suggest a plausible way in which phenolic substances might enter into the path of hydrogen transfer in plants.

The data to be presented in this paper embody a study of the polyphenolase system in apples. Investigations have been carried out on the respiration of sliced apple tissue supplied with various enzymic substrates and inhibitors. The properties of a crude preparation of polyphenolase from apples have also been studied. The data presented indicate that this enzyme is probably very important in the respiratory metabolism of apples.

MATERIALS AND METHODS.

Most of the fruits used were immature and mature Granny Smith apples of the 1945 and 1946 seasons obtained from a selected orchard at Orange, N.S.W. The mature fruits were part of the mid-April (commercial) picking and were placed in cool store (1°C.) within a few days of harvesting. Samples were withdrawn from store as required and placed in a room maintained at 25°C., at which temperature all subsequent work was carried out. Immature fruits were placed at 25°C. without previous cool storage.

In the earliest experiments fruits of the 1944 season were used. These had been in cool store for 4-5 months.

Investigation of the Respiratory Metabolism of Tissue Slices.—In the investigation of the respiratory metabolism of tissue slices the technique described in a previous publication (Hackney, 1945) was used. It was found inadvisable to use a calcium chloride medium in this work, as the presence of this salt apparently prevented protocatechuic acid (an important substrate for polyphenolase) from being utilized by the cells; a solution of potassium nitrate isotonic with the cell sap was therefore used instead of the calcium chloride solution recommended in previous descriptions of the technique. Potassium nitrate did not appear to have any marked effect on the endogenous respiration of the tissue slices, nor did it appear to hinder or enhance the effect of protocatechuic acid on respiration.

The reason for the effect of calcium chloride on the utilization of protocatechuic acid was not discovered. It was not that the pH of the solution was unfavourable for absorption, since protocatechuic acid was readily taken up from solutions of potassium nitrate and other salts having approximately the same pH as the calcium chloride solution.

Possible respiratory substrates were added to the media in the central cavities of the Warburg vessels from the sidearms. The inhibitor resorcinol was added in the same way. It was not practicable to add potassium cyanide in this way; free HCN from solution placed in the sidearm would gradually have been absorbed by the medium in the central cavity, resulting in partial inhibition of the respiration of the tissue before the addition of the solution in the sidearm to the medium. The required concentration of neutralized potassium cyanide was therefore added to the medium at the beginning of the experiment.

Special precautions were necessary when the Warburg vessels contained alkali for the absorption of carbon dioxide. The absorption of free HCN by the alkali would have led to serious errors in the manometric readings. These errors were avoided by substituting for alkali an alkali-cyanide mixture in which the concentration of free HCN was equal to the concentration in the experimental medium. The appropriate KOH-KCN mixtures are given by Krebs (1935).

Preparation of Crude Polyphenolase.—A crude extract of polyphenolase was prepared using a method similar to that of Kubowitz (1937). Previously frozen apple tissue (skin and flesh) was washed and the mash was extracted with ice-cold M/10 phosphate buffer at pH 7.4 (100 ml. to 250 gm. tissue). Kubowitz extracted polyphenolase from potatoes with ice-cold water. Owing to the sap of apples being much more acid than that of potatoes, it was found necessary to use a buffer solution instead of water in order to keep the pH of the extract above the isoelectric point of the protein. The pH of freshly-prepared apple juice (determined by means of a glass electrode) was 3.67, at which value the activity of the enzyme was impaired. The crude extract in phosphate buffer was filtered through cotton wool and subsequently filtered by suction through No. 1 Whatman paper. Sufficient ice-cold acetone was added to the filtrate to make the acetone content equal to 40% of the total volume; the precipitate which formed was centrifuged off and discarded. The acetone content was then increased to 55%. The precipitate which formed contained the enzyme. It was centrifuged off (10 minutes at 2,500 rev./min.) and dissolved in a volume of water equivalent to one-fifth of the volume of the original extract. Owing to the precipitation of pectic substances with the enzyme, the volume of water necessary for the solution of crude apple polyphenolase was greater than that used by Kubowitz for potato enzyme. The supernatant liquid left after removal of the precipitate had no polyphenolase activity. All the operations during the extraction of the enzyme were carried out at 0°C. The enzyme preparation could be stored for many months at 0°C. with very little loss of activity. Its properties were studied at 25°C.

EXPERIMENTAL RESULTS.

(A) WITH CUT TISSUE.

The following notation is used throughout this section:

QO_2 = rate of uptake of oxygen (mm.³/gm.fr.wt./hr.).

QCO_2 = rate of output of carbon dioxide (units as above).

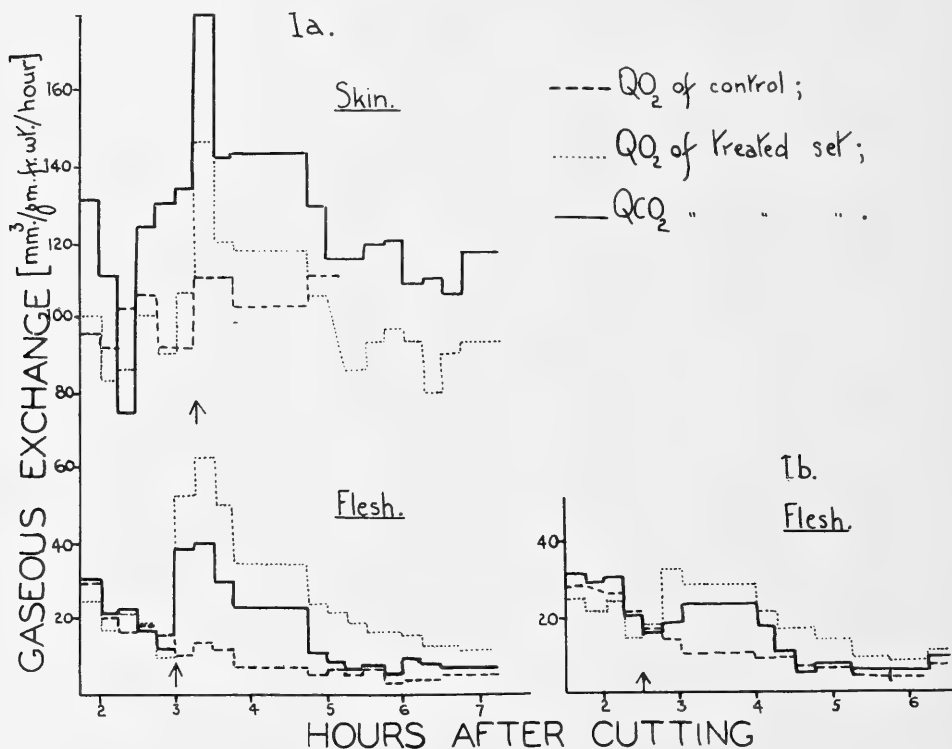
R.Q. = respiratory quotient, i.e. ratio QCO_2/QO_2 .

EFFECTS OF ADDITION OF PROTOCATECHUIC ACID AND OTHER PHENOLIC SUBSTANCES TO CUT TISSUE.

Addition of protocatechuic acid to the medium surrounding flesh or skin resulted in a rapid increase in QO_2 to a maximum value, followed by a fall towards the control level. In those experiments for which senescent apples of the 1944 season were used QCO_2 was not determined.

Behaviour of Immature Apples of the 1945 Season.—Addition of protocatechuic acid to skin or flesh of very immature apples of the 1945 season brought about a rapid rise in both QO_2 and QCO_2 (see Text-fig. 1a). The pH at which the protocatechuic acid was added to the medium was between 3.6 and 3.7, whether the medium was potassium nitrate or water; the addition of protocatechuic acid did not alter the pH by more than 0.1 or 0.2 unit. The pH of the medium was checked at the close of the experiment. The R.Q. of flesh tissue after treatment was less than unity. After the maximum QO_2 and QCO_2 had been maintained for 15–30 minutes the values fell slowly towards the control levels. In the skin the QO_2 and QCO_2 frequently fell below the control levels after the maxima had been passed, but in the flesh they remained higher than the control levels until the close of the experiment (more than five hours after treatment). It was found that the amount of extra oxygen taken up by flesh tissue after addition of 0.5 mg. of protocatechuic acid to the medium was more than 146 mm.³

(i.e., it was equal to 146 mm.³ and still increasing when the experiment was concluded). The theoretical amount of oxygen required for the complete oxidation of 0.5 mg. of protocatechuic acid was only about 84 mm.³ (assuming two atoms of oxygen taken up for every molecule of protocatechuic acid oxidized). Evidence that the protocatechuic acid penetrated to the inner cells of the tissue slices, rather than remaining in the superficial cut cells, was provided by the fact that the brown quinonoid products of its oxidation extended right through the tissue.



Text-figures 1a and 1b.

Fig. 1a shows respiratory behaviour of skin and flesh of very immature apples of the 1945 season in the presence of added protocatechuic acid.

Fig. 1b shows respiratory behaviour of flesh from slightly older apples of the 1945 season in the presence of protocatechuic acid.

As the apples advanced in maturity changes were observed in the behaviour of the tissues towards added protocatechuic acid. Both QO₂ and QCO₂ increased after treatment, but the control level was frequently regained when the amount of extra oxygen taken up was very little greater than the theoretical amount required for the oxidation of the protocatechuic acid added (see Text-fig. 1b).

Behaviour of Immature Apples of the 1946 Season.—Immature apples of the 1946 season differed from those of the 1945 season in their behaviour towards added protocatechuic acid. After addition of protocatechuic acid to the medium surrounding skin or flesh the QO₂ rose rapidly. The rise in QO₂ was sometimes accompanied by a rise in QCO₂. The QO₂ and QCO₂ were not maintained above the control levels for more than a few hours after treatment. The amount of extra oxygen taken up (i.e. oxygen taken up in excess of the normal control amount) was only slightly greater than the theoretical amount required for the complete oxidation of the substrate added.

The effects of addition of protocatechuic acid to the medium surrounding cut skin were nearly always similar to those produced in flesh tissue, but in two experiments

it was observed that addition of protocatechuic acid to cut skin had very little effect either on QO_2 or on QCO_2 .

Behaviour of Mature Apples of the 1945 and 1946 Seasons.—Addition of protocatechuic acid to the media surrounding skin or flesh from apples of commercial maturity resulted in an increase in QO_2 nearly always unaccompanied by a rise in QCO_2 . The observed amount of oxygen taken up by the tissue after treatment was no greater than the theoretical amount required for the oxidation of the acid added. In a few experiments with very senescent apples QCO_2 as well as QO_2 was temporarily increased (cf. some of the immature apples mentioned above).

Effects of Addition of Phenolic Substrates other than Protocatechuic Acid.—Protocatechuic acid was the only phenolic substrate supplied to tissues from immature apples, but the effects of addition of catechol and of p-cresol to tissues from mature apples were observed. Both the o-dihydroxy phenol and the monohydroxy phenol were rapidly oxidized when added to the media surrounding flesh tissue. Catechol was oxidized more rapidly than either protocatechuic acid or p-cresol. Addition of a second dose of protocatechuic acid, catechol or p-cresol resulted in a second increase in QO_2 , which, however, was not as great as the increase shown after addition of the first dose.

EFFECTS OF RESPIRATORY INHIBITORS ON THE POLYPHENOLASE OF CUT APPLE TISSUE.

Effects of Addition of Resorcinol.—Richter (1934) studied the inhibition of potato polyphenolase by various substances, including resorcinol. When resorcinol in various concentrations was added to the media surrounding apple skin or flesh, partial inhibition of respiration was evident within half an hour of treatment. The addition of resorcinol (0.1M) did not alter the pH of the medium by more than 0.1 unit. Text-fig. 2 shows the respiratory behaviour of skin and flesh treated with two concentrations of resorcinol. Several concentrations of resorcinol were used in various experiments. The minimum concentration required for complete or almost complete inhibition of flesh respiration was only 0.025M. Maximum (100%) inhibition of flesh and a half hours after treatment. Treatment of skin with 0.05M resorcinol caused approximately 50% inhibition of respiration after one hour, and no further inhibition took place. The minimum concentration of resorcinol required for the complete inhibition of flesh respiration was only 0.025M. Maximum (100%) inhibition of flesh respiration by 0.025M, 0.05M and 0.1M resorcinol was observed two to two and a half hours after treatment.

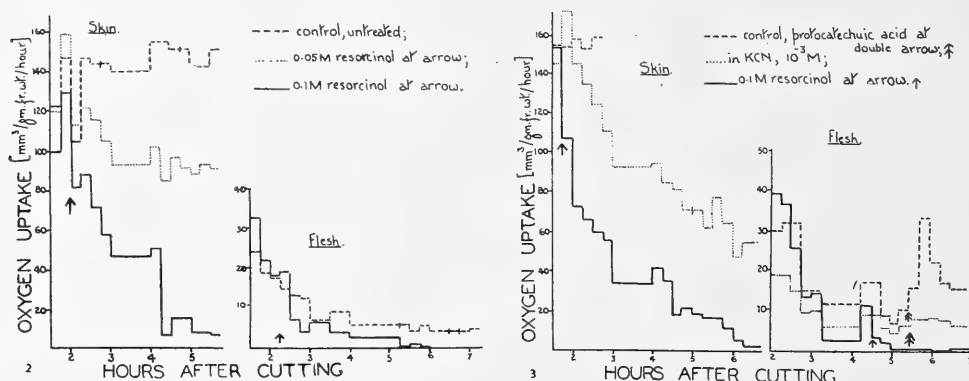
Richter considered that resorcinol acted as a simple competitive inhibitor of the polyphenolase of potatoes, as the amount of inhibition could be reduced by increasing the substrate concentration. When excess protocatechuic acid was added to the medium surrounding apple tissue which had been treated with resorcinol, the respiration rate, as measured by QO_2 , was increased, but not to the same extent as it was increased in tissues which had not been treated with resorcinol; the *percentage* inhibition was not reduced in the presence of excess protocatechuic acid.

Effect of Treatment with Potassium Cyanide.—When skin or flesh was immersed in 10^{-3} M potassium cyanide neutralized with dilute sulphuric acid, partial inhibition of QO_2 was observed within the first hour after treatment. Maximum inhibition of flesh respiration was not observed until two or more hours after immersion in KCN. Four or five hours were required for the percentage inhibition of the respiration of skin to reach its maximum value. The maximum percentage inhibition of skin or flesh respiration by 10^{-3} M KCN varied between approximately 50% and 75% for different apples. The maximum percentage inhibition was much higher when 10^{-2} M cyanide was used instead of 10^{-3} M. In experiments where 10^{-2} M cyanide failed to inhibit respiration completely, further inhibition was brought about by the use of 10^{-1} M cyanide. Table 1 gives typical values for tissues immersed in various concentrations of potassium cyanide.

TABLE 1.
Effects of Various Concentrations of Potassium Cyanide on QO_2 of Skin and Flesh.

No. of Experiment.	Tissue.	Concentration of KCN.	Minimum QO_2 of Treated Tissue.	Minimum QO_2 of Control Tissue.	Percentage Inhibition.
1	Skin	$10^{-2}M$	65	126.0	48.4
1	Flesh	$10^{-2}M$	6	12.5	52.0
2	Skin	$10^{-2}M$	50	153.0	67.3
2	Flesh	$10^{-2}M$	6	12.0	50.0
3	Skin	$10^{-2}M$	19.7	199.0	90.0
3	„	$10^{-2}M$	0.0	199.0	100
3	Flesh	$10^{-2}M$	0.0	4.2	100
3	„	$10^{-1}M$	0.0	4.2	100

Text-figure 3 shows a comparison between the effects of $10^{-2}M$ potassium cyanide and of 0.1M resorcinol on the respiration of skin and flesh. In the presence of KCN protocatechuic acid was not oxidized by the tissue. It would be difficult, of course,



Text-figures 2 and 3.

Fig. 2.—Respiratory behaviour of skin and flesh treated with two concentrations of resorcinol.

Fig. 3.—Comparison between the effects of $10^{-2}M$ potassium cyanide and of 0.1M resorcinol on the respiration of skin and flesh. In the presence of cyanide, addition of protocatechuic acid had no effect on respiration.

to ascertain whether this was due to an effect of KCN on the permeability of the tissue to protocatechuic acid or to a direct effect of KCN on the polyphenolase in the cells. Data to be presented in a later section show that KCN does inhibit the activity of apple polyphenolase *in vitro*.

(B) PROPERTIES OF THE ENZYME PREPARATION.

The crude enzyme preparation was made from mature Granny Smith apples of the 1946 season. The total volume of enzyme extract from each sample of three apples (about 400 gm. fr. wt.) was about 20 ml. (about 52 mg. dry wt.). The specific activity of the preparation towards catechol,

$$W = \frac{\text{mm.}^3 \text{ oxygen taken up}}{\text{dry wt. enzyme (mg.)} \times \text{time (minutes)}}$$

at pH 7.4 and 25°C., was approximately 1.4. This figure compared favourably with that given by Kubowitz (1937) for crude polyphenolase from potatoes ($W = 3$ to 5).

Activity of the Enzyme Preparation towards Catechol.—The enzyme preparation was used in M/10 phosphate buffer, pH 7.4; it showed no appreciable oxygen uptake in the absence of added substrate. When catechol or protocatechuic acid was added to the enzyme solution at pH 7.4, rapid oxidation of the substrate proceeded for a short time (15 minutes or less), after which the enzyme apparently became inactive. No further oxidation occurred when a second dose of substrate was added. Richter (1934), working with polyphenolase from potatoes, pointed out that the o-quinones formed by the primary oxidation of catechol derivatives can effect the secondary oxidation of various substances, one of which is o-phenylenediamine. When o-phenylenediamine was added by the present writer to the system apple polyphenolase plus substrate, after the inactivation of the enzyme had taken place, the inactivation was reversed and the oxidation of substrate was resumed. If the o-phenylenediamine was added simultaneously with the catechol (or other substrate) no inactivation of the enzyme took place. The system enzyme + catechol + o-phenylenediamine took up an amount of oxygen approximately equal to the theoretical amount required for the complete oxidation of the amount of catechol added. If, after the complete oxidation of the first dose of catechol had taken place, a second dose of catechol plus o-phenylenediamine was added, it was readily attacked by the enzyme. In all subsequent experiments inactivation of the enzyme was prevented by the addition of sufficient o-phenylenediamine to combine with all the quinone formed by the oxidation of the substrate. The enzyme did not attack o-phenylenediamine, neither did the presence of o-phenylenediamine cause oxidation of the substrate in the absence of enzyme.

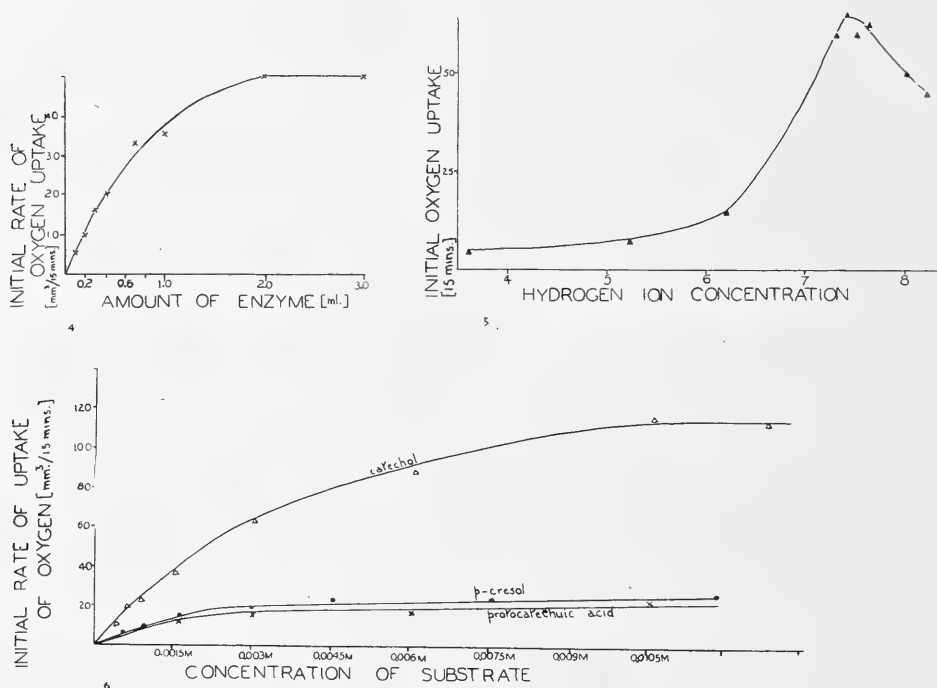
Text-figure 4 shows the effect of varying enzyme concentration (at pH 7.4) on the rate of oxidation of a mixture of 2 mg. catechol with 2 mg. o-phenylenediamine. The initial rate of oxidation of catechol was roughly proportional to the enzyme concentration when the amount of enzyme present did not exceed 0.7 ml. solution; at higher concentrations of enzyme this proportionality broke down. The dose of catechol used in subsequent experiments was 2 mg., unless otherwise stated. When enzyme concentration was intended to be the limiting factor in determining rate of oxidation of substrate, volumes of enzyme solution less than 0.7 ml. were used; where substrate was to be the limiting factor, 2 ml. or more of the enzyme solution were used in each replicate.

Causes of Inactivation of Enzyme during Oxidation of Catechol.—There has been considerable controversy regarding the cause of the inactivation of polyphenolase during the oxidation of catechol and other substances. Richter (1934) considered that the o-quinone formed during the oxidation of catechol by potato polyphenolase was probably responsible for the inactivation of the enzyme, since inactivation was greatly reduced by the addition of substances such as aniline and o-phenylenediamine which combined with the o-quinone. Ludwig and Nelson (1939) disagreed with Richter's view because of two observations: (1) that addition of ascorbic acid, which is also capable of reducing o-quinone, did not prevent the inactivation of the enzyme; (2) that in one of their experiments "the enzyme was allowed to react with only a fraction of the amount of catechol necessary to inactivate it completely; the active enzyme remaining after the oxidation of this initial addition was shaken in the Warburg apparatus for 40 minutes in the presence of the o-benzoquinone previously formed, and then an excess of catechol was added to the reaction vessel, whereupon further consumption of oxygen occurred. The total oxygen uptake was found to be the same as in the case of the control in which the enzyme was allowed to react on an excess of catechol at the start."

However, the present writer wishes to draw attention to the fact that the second observation cannot be taken as evidence that o-benzoquinone had no inhibitory effect on polyphenolase. Earlier in their paper Ludwig and Nelson had shown that complete inactivation of the enzyme did not take place until a certain amount of oxygen had been taken up. This amount was constant for each type of polyphenolase preparation made by them (they used enzyme prepared from various plant sources). The amount of o-quinone formed by the enzyme during the oxidation of "a fraction of the catechol necessary to inactivate it completely" was by this very definition insufficient to cause

complete inhibition. All that can be inferred from observation (2) above is that polyphenolase is not completely inactivated until the inhibitory products of reaction have reached a certain concentration.

As with the enzyme preparations used by Ludwig and Nelson, ascorbic acid had little or no protective action on the polyphenolase of apples. However, it is possible that the affinity of ascorbic acid for the quinone was much less than that of *o*-phenylenediamine and that some quinone may have remained attached to the enzyme even in the presence of ascorbic acid. The writer undertook several experiments in an attempt to observe directly the effects of *o*-quinone on the activity of apple polyphenolase towards catechol at pH 7.4 and 25°C. The *o*-benzoquinone was prepared by the method of Wilstätter and Pfannensteil (1904) and used immediately after preparation. In one of these experiments *o*-quinone appeared to retard the oxidation of catechol, but unfortunately this result could not be repeated. *O*-benzoquinone is difficult to prepare; Wilstätter and Pfannensteil report frequent failures in preparation. In addition, it is a very unstable substance and is likely to undergo alteration when dissolved in water.



Text-figures 4-6.

Fig. 4.—The effect of varying enzyme (polyphenolase) concentration at pH 7.4 on the rate of oxidation of a mixture of 2 mg. catechol with 2 mg. *o*-phenylenediamine.

Fig. 5.—Activity of apple polyphenolase in buffers of various pH. substrate supplied was 2 mg. catechol plus 2 mg. *o*-phenylenediamine.

Fig. 6.—Rates of oxidation of catechol, *p*-cresol and protocatechuic acid as functions of the amount of substrate added to polyphenolase preparation. These data were obtained in a typical experiment.

Effects of Changes in Hydrogen Ion Concentration on the Activity of the Enzyme Preparation towards Catechol.—The enzyme was very sensitive to changes in the pH of the buffer solution surrounding it. Activity towards 2 mg. of catechol in the presence of 2 mg. of *o*-phenylenediamine was determined at 25°C. in buffers having a pH range from 3.6 to 8.2 inclusive. Acetate buffers were used from 3.6 to 5.6 inclusive, phosphate buffers from 5.6 to 7.8 inclusive, and glycine buffers from 7.8 upwards.

Close agreement between values for activity at pH 7.8 in phosphate and in glycine, and between values at pH 5.6 in phosphate and in acetate showed that the effects observed were due to changes in pH and not to differences in the type of buffer used. Text-figure 5 shows the behaviour of the enzyme in buffers of various pH. The enzyme preparation showed very slight activity below 4.5; above 4.5 the activity increased, reaching its optimum between 7.4 and 7.8; between 7.8 and 8.2 there was a slight decrease in activity; above pH 8.2 the substrate was found to be readily autoxidizable in air.

Effects of Variation in Substrate Concentration.—For low concentrations of catechol (1 mg./6 ml., = 0.0015M, or less) the initial rate of oxidation by excess enzyme (3 ml. enzyme preparation) was roughly proportional to the amount of substrate present; this proportionality broke down when the concentration of catechol was increased beyond 0.0015M. The maximum rate of oxidation was reached when 3 ml. of enzyme preparation were supplied with 8–9 mg. catechol. Text-figure 6 shows the rate of oxidation of catechol as a function of the amount of substrate added.

MICHAELIS CONSTANTS AND AFFINITY OF THE ENZYME FOR VARIOUS SUBSTRATES.

The effect of substrate concentration on the initial velocity of an enzyme-catalysed reaction is probably of very great significance. Michaelis and Menten (1913) were the first to explain the rectangular hyperbolic shape of the typical substrate-velocity curve. These workers assumed that the enzyme, E, and the substrate, S, combined to form an intermediate product, ES, which then dissociated to give free enzyme and final products of the reaction. The dissociation constant of the enzyme-substrate complex ES can then be taken as being equal to the substrate concentration at which half the maximum velocity is reached. This dissociation constant is known as the Michaelis constant and is denoted by the symbol K_m . Michaelis and Menten's method of estimating K_m is useful only when the maximum velocity, V , is known with some degree of accuracy.

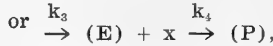
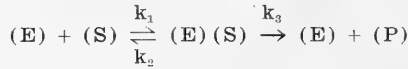
Lineweaver and Burk (1934) developed the theory of Michaelis and Menten to include more complex mechanisms than those considered by the original workers. When the method of Lineweaver and Burk is adopted it is not necessary to determine the value of V by observation in order to determine K_m . The reciprocal of the initial velocity of reaction ($1/V$) plotted against the reciprocal of substrate concentration ($1/S$) results in a straight line with slope equal to K_m/V and an ordinate intercept equal to $1/V$; V and K_m can readily be estimated from these values.

Text-figure 7 shows the application of the treatment developed by Lineweaver and Burk to the data obtained when various concentrations of catechol were supplied to apple polyphenolase. The maximum velocity, calculated from the value for the ordinate intercept, was 533 mm.³ of oxygen per hour; this figure agreed well with the observed value, 504 mm.³ per hour. The value for K_m calculated from the slope of the line was equal to 0.0056.

The relative activities of the enzyme preparation towards protocatechuic acid and towards p-cresol were also studied. Rates of oxidation of these substances are presented as a function of substrate concentration in Text-figure 6. Both substances were readily attacked by the enzyme. The rate of uptake of oxygen after addition of a given concentration of p-cresol was of the same order as the rate of oxygen uptake after addition of the same concentration of protocatechuic acid; both these rates were much slower than that observed after addition of the same concentration of catechol. Treatment of the data by the method of Lineweaver and Burk gave values for V and K_m as shown in Table 2.

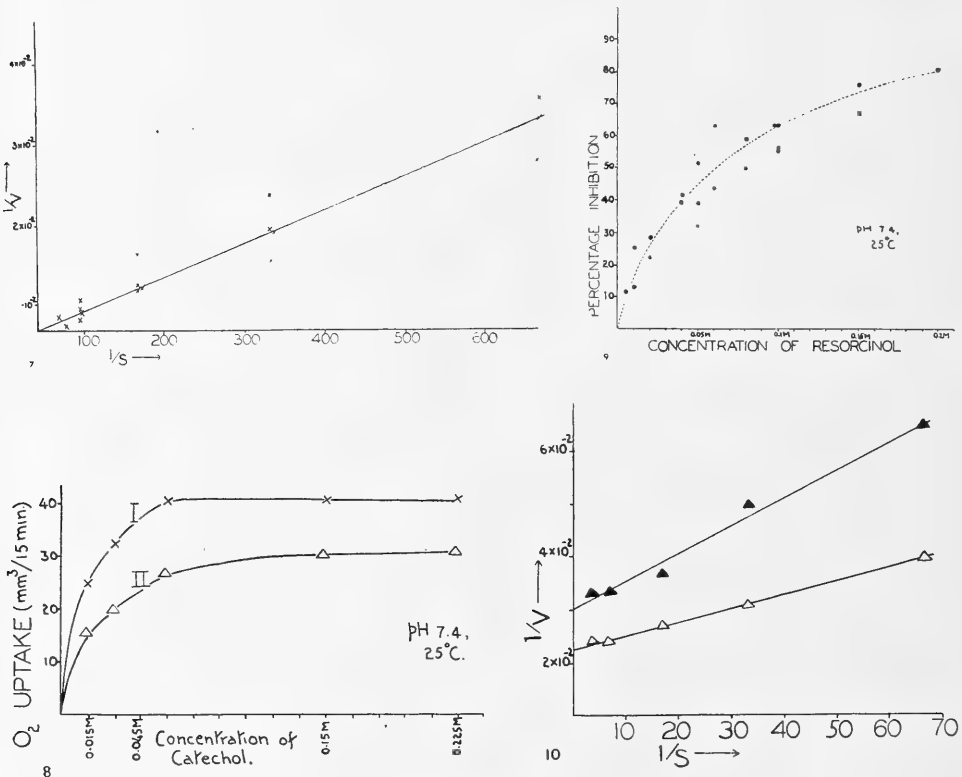
The affinity of polyphenolase for each of its substrates was taken as the reciprocal of the Michaelis constant for that substrate. It was found that the affinity of the enzyme for p-cresol was approximately equal to its affinity for protocatechuic acid; the affinity of the enzyme for either of these substrates was about twenty-eight times as great as its affinity for catechol. As has already been mentioned, the observed rates of oxidation of p-cresol and of protocatechuic acid were much slower than the rate of oxidation of catechol. Since the affinities of the enzyme for p-cresol and protocatechuic acid were so much greater than its affinity for catechol, it must be assumed

that the slower rates of oxidation of the first two substrates were due to the slowness, not of the rate of formation of the enzyme-substrate complex, but of the rate of some subsequent stage of the oxidation to give free enzyme plus products. If (E) is the concentration of enzyme and (S) is the concentration of substrate, then



where k_1 , k_2 , k_3 and k_4 are the dissociation constants for the reactions involved and (P) is the concentration of the end product.

If the first of these equations is true, then $\frac{V \text{ catechol}}{V \text{ protocatechuic acid}}$ is a measure of $\frac{k_3 \text{ catechol}}{k_3 \text{ protocatechuic acid}}$ where substrate concentration and oxygen supply are infinite.



Text-figures 7-10.

Fig. 7.—Application of the treatment developed by Lineweaver and Burk to the data obtained when various concentrations of catechol were supplied to apple polyphenolase.

Fig. 8.—Rates of oxygen uptake by apple polyphenolase in the presence of varying concentrations of catechol (plus o-phenylenediamine). The higher curve (I) shows the behaviour of the enzyme in the absence of inhibitor; the lower curve (II) shows its behaviour in the presence of 0.1M resorcinol. The concentrations supplied here were much greater than those used in Fig. 6.

Fig. 9.—Percentage inhibition of the activity of apple polyphenolase towards a standard concentration of catechol (0.003M) plotted against concentration of resorcinol used.

Fig. 10.—Reciprocals of the initial velocities of oxidation plotted against reciprocals of substrate concentration. The dark triangles represent observations made in the presence of 0.1M resorcinol, the light triangles represent observations made in the absence of inhibitor.

The rate of breakdown of the polyphenolase-catechol complex might have been about five times as great as that of the polyphenolase-protocatechuic acid complex.

EFFECTS OF INHIBITORS ON THE ACTIVITY OF THE ENZYME PREPARATION.

Inhibition by Resorcinol.—Richter (1934) considered that inhibition of potato polyphenolase by resorcinol was of the simple competitive type, "since it could be reduced by increasing the substrate concentration". Resorcinol differs from catechol

TABLE 2.
Michaelis Constants and Maximum Velocities of Reaction for Apple Polyphenolase Supplied with Various Substrates.

Substrate.	Km (Method of L. and B.).	Km (Method of M. and M.).	Affinity of Enzyme for Substrate.	V (Calculated).	V (Observed).
Catechol	0.0056	0.0045	178.5	533	504
Protocatechuic acid	0.0002	0.0002	5000.0	89	100
p-cresol	0.0002	0.0002	5000.0	133	120

V is expressed in mm.³ oxygen/hour.

only in the position of the second hydroxyl group; catechol is o-dihydroxy benzene and resorcinol is m-dihydroxy benzene. It is therefore easy to imagine resorcinol competing with catechol for the active group of the polyphenolase molecule.

TABLE 3.
Inhibition of Activity of Apple Polyphenolase Towards Catechol in the Presence of 0.1 M Resorcinol.

Concentration Catechol.	Oxygen Uptake.		Percentage Inhibition.
	No Resorcinol.	0.1 M Resorcinol.	
0.015 M	25.0	15.5	40.8
0.03 M	32.5	20.0	42.8
0.06 M	40.5	27.0	32.5
0.15 M	41.0	30.5	26.8
0.225 M	41.0	30.5	26.8

From the nature of competitive inhibition it is clear that percentage inhibition by a constant amount of inhibitor should decrease when substrate concentration is increased. When the rates of oxygen uptake by the enzyme preparation in presence and absence of a given concentration of inhibitor are plotted against concentration of substrate supplied, the two curves should tend to converge as substrate concentration is increased. Text-figure 8 shows the rates of oxygen uptake by apple polyphenolase in the presence of varying concentrations of catechol (plus o-phenylenediamine). The higher curve (I) shows the behaviour of the enzyme in the absence of inhibitor; the lower curve (II) shows its behaviour in the presence of 0.1M resorcinol. The concentrations of substrate supplied here were much greater than those used in Text-figure 6. The points plotted represent mean values from several experiments. The concentrations of resorcinol and substrate used did not significantly alter the pH of the system. The two curves in Text-figure 8 appear to diverge slightly from each other when the concentration of catechol is less than 0.06M. They converge slightly as the concentration of catechol is increased from 0.06M to 0.15M, then appear to run parallel to each other as the substrate concentration is increased from 0.15M to 0.225M. There is in fact no apparent difference in the respective rates of oxygen uptake, with and without resorcinol, over this latter range of substrate concentration.

It is possible that the curves are still convergent, but at such a slow rate as to appear to be parallel to each other. If this were so, resorcinol could be described as a competitive inhibitor whose competitive nature does not become evident until the substrate concentration has been raised to a relatively high level. Table 3 shows the percentage inhibition by 0.1M resorcinol in the presence of various concentrations of catechol.

Text-figure 9 shows the percentage inhibition of the activity of apple polyphenolase towards a standard concentration of catechol (0.003M) plotted against concentration of resorcinol used. If the inhibition were non-competitive the points should approximate to a straight line; if it were competitive they should approximate to a curve. The competitive nature of the inhibition does not become evident in Text-figure 9 until the substrate concentration is increased above 0.1M.

When the reciprocals of the initial velocities of oxidation in the presence of inhibitor are plotted against the reciprocals of the substrate concentrations, a straight line is obtained (see Text-figure 10). Lineweaver and Burk (1934) showed that competitive inhibition is indicated by an increase in the slope of the $1/v:1/s$ plot, compared with that given in the absence of inhibitor. The difference in slope between the two straight lines in Text-figure 10 is therefore in accordance with the behaviour of a competitive inhibitor.

The dissociation constant of the enzyme-inhibitor complex, K_i , can be calculated from the relationship $K_s + \frac{K_s(I)}{K_i} = V$ times the slope of the line, where (I) is the

concentration of the inhibitor and K_s is the dissociation constant of the enzyme-substrate complex as determined in the absence of inhibitor. When catechol was used as substrate and 0.1M resorcinol as inhibitor, the value obtained for K_i was 0.000002.

The dissociation constant of the polyphenolase-resorcinol complex was very much smaller than those of the polyphenolase-catechol and polyphenolase-protocatechuic acid complexes (0.0056 and 0.0002 respectively). The affinity of the enzyme for resorcinol ($1/K_i$) is about 2,800 times as great as its affinity for catechol and 100 times as great as its affinity for protocatechuic acid or p-cresol. This high relative affinity for resorcinol would account for the fact that the competitive nature of the inhibition does not become evident until the substrate concentration is increased to a relatively high value.

TABLE 4.
Inhibition of Crude Apple Polyphenolase by Various Concentrations of Potassium Cyanide.

Concentration of KCN.	Oxidation of Catechol by Control (mm. ³ O ₂ /15 min.).	Oxidation of Catechol after Treatment.	Percentage Inhibition.
10 ⁻⁵ M	35.3	37.3	0
10 ⁻⁴ M	35.3	28.0	20.7
10 ⁻³ M	35.3	24.0	32.0
10 ⁻² M	24.0	12.0	50.0
10 ⁻¹ M	35.3	3.0	91.5
10 ⁻² M	10.3	0.0	100
10 ⁻¹ M	10.3	0.0	100

Inhibition by Potassium Cyanide.—Potassium cyanide has long been recognized as an inhibitor of iron and copper enzymes. Kubowitz (1937) reported that potato polyphenolase was very sensitive to this poison. Polyphenolase from apples was treated with various concentrations of neutralized potassium cyanide. It was found to be less sensitive to cyanide than polyphenolase from other sources mentioned in the review of Nelson and Dawson (1944). The maximum inhibition was not evident until three to four hours after treatment. Typical data for the inhibition of the oxidation of catechol by various concentrations of cyanide are shown in Table 4.

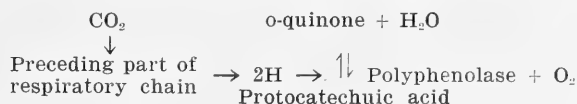
Potassium cyanide at concentrations of $10^{-2}M$ or less had no inhibitory effect on the oxidation of catechol by apple polyphenolase; at $10^{-4}M$ a slight effect was observed; at $10^{-3}M$ the amount of inhibition varied between one-third and one-half of the total rate of oxidation. It was not until the concentration of KCN was raised to $10^{-2}M$ that extreme sensitivity was manifested by the enzyme.

GENERAL DISCUSSION.

The Effects of Treatment of Apple Tissue with Various Phenols.—The behaviour of flesh from immature apples of the 1945 season suggested that protocatechuic acid was acting as a respiratory catalyst. The strongest pieces of evidence in favour of this theory were: (a) both QO_2 and QCO_2 were increased by the addition of protocatechuic acid to the media surrounding the tissues, and (b) much more oxygen was taken up than was necessary for the complete oxidation of the protocatechuic acid added.

Observation (a) was similar to the findings of Boswell and Whiting (1938) and of Baker and Nelson (1943), who reported increased oxygen uptake and carbon dioxide output by potato tissue after treatment with catechol and with protocatechuic acid. Baker and Nelson also found that after addition of protocatechuic acid to potato tissue more oxygen was taken up than was required for the oxidation of the protocatechuic acid added. Walter and Nelson (1945), working with sweet potato tissue supplied with various phenols, observed effects similar to those observed by Baker and Nelson with potato tissue.

Catechol and p-cresol as well as protocatechuic acid were readily oxidized by tissue from mature apples. However, the evidences of catalytic effects exhibited by tissue from immature apples were usually not shown by tissue from mature apples. It is possible that the immature apples used were poor in phenolic substrate but contained respiratory enzymes in abundance. If this had been true, addition of phenolic substrate to tissue from immature apples could have resulted in oxidation of the substrate to o-quinone and water, followed by the subsequent reduction of the quinone by two atoms of hydrogen passed along the preceding part of the respiratory chain. The acceptance of hydrogen by the quinone would have resulted in speeding up the action of the preceding part of the respiratory chain, causing an increase in QCO_2 , provided that there was no lack of the substrates and enzymes necessary for it to function. Thus protocatechuic acid could have been acting catalytically in a cycle such as this:



Addition of phenolic substrate to the tissues of mature apples, or of those immature apples which resembled mature apples in their behaviour, would have resulted in oxidation of the substrate to o-quinone, provided that there was sufficient polyphenolase present to enable the oxidation to proceed. Subsequent reduction of the o-quinone might have been impossible because the rate of action of the preceding part of the respiratory mechanism was being limited by the concentration of one or more of the enzymes or substrates necessary for it to function. Thus the absence of catalytic effects after addition of phenolic substrate to tissues from some apples did not necessarily mean that phenolic substrate was incapable of bringing about catalytic effects in other apples.

Boswell (1945) considered that there was more than one oxidase concerned in the respiration of potato tissue. The fraction of the respiration which was dependent on polyphenolase was, according to him, limited by the amount of polyphenol in the cells. When excess substrate was supplied the amount of hydrogen donator present became the limiting factor. Boswell found that the amino acids were capable of reducing the o-quinone formed by the action of polyphenolase and therefore of causing an increase in both QO_2 and QCO_2 . Non-nitrogenous organic acids, such as succinic acid, appeared to retard the excess QCO_2 in the presence of added substrate. Boswell considered that non-nitrogenous organic acids probably reduced the amount of H-donator available to

react with the quinone. Preliminary investigations by the present writer on the effects of organic acids, such as malic, citric and succinic acids, indicate that an organic acid cycle may be important in the respiratory metabolism of the apple. The presence of succinate did not, however, appear to influence the effect produced on respiration of apple tissue by the addition of protocatechuic acid. The only amino acid tried was aspartic acid. When added simultaneously with protocatechuic acid, aspartic acid did not alter the QCO_2 . More work must be done to ascertain the roles of the various organic acids in the respiration of apple tissue; at present it appears that the behaviour of apple tissue was different from that of potato tissue in the presence of these substances.

Inactivation of polyphenolase during the oxidation of phenolic substrates was much slower *in vivo* than *in vitro*. It was not necessary to add o-phenylenediamine in order that polyphenolase in cut tissue might oxidize all the substrate added. It is possible that the reaction products were modified *in vivo* too rapidly for them to have exerted a detrimental effect on the enzyme.

The effects of maturity on the reactions of the tissues to the addition of phenolic substrate cannot be adequately explained in the light of our present knowledge. Bennet-Clark and Bexon (1943) reported somewhat similar seasonal variations in the response of beet tissue to the addition of beet juice or of salts of organic acids such as malate.

Evidence of the Importance of Polyphenolase from Effects of Inhibitors.—The effects of resorcinol on the respiration of cut apple tissue indicated that the greater part, if not the whole, of the oxygen uptake was dependent on the action of polyphenolase. Polyphenolase is the only oxidase known to be inhibited by resorcinol.

Potassium cyanide is known to inhibit cytochrome oxidase, ascorbic acid oxidase from some sources, and polyphenolase. Attempts to isolate cytochrome oxidase from apples by the method of Goddard (1944) were unsuccessful; cytochrome oxidase is therefore probably absent from apples. The ascorbic acid oxidase isolated from apples by the writer (Hackney, 1946) was found to be extremely sensitive to cyanide, complete inhibition of its activity being brought about by treatment with a $10^{-3}M$ solution. Any fraction of the respiration of cut tissue which depended on the activity of ascorbic acid oxidase would therefore probably have been inhibited by treatment with cyanide at a concentration of $10^{-3}M$. The respiration of cut apple tissue was not completely inhibited until the concentration of cyanide was increased to $10^{-2}M$ or $10^{-1}M$. The same high concentrations of potassium cyanide were necessary for the complete inhibition of the activity of the polyphenolase preparation.

Potential Quantitative Activity of Polyphenolase in Apples.—The rate at which oxygen could be taken up by polyphenolase in the presence of excess substrate was dependent on the pH of the medium. The pH of freshly prepared juice from mature Granny Smith apples was 3.67. Polyphenolase could not be prepared from apples of this pH. The isolated enzyme showed very little activity at pH 3.6 and was very unstable at any pH below 5.0. Very low hydrogen ion concentrations are known to be destructive to many enzymes. In view of these facts it must be concluded that either (a) polyphenolase and many other enzymes are incapable of participating to any great extent in the enzymic activity necessary for the maintenance of cellular metabolism or (b) the pH of the expressed juice is much lower than the pH of the cytoplasm at the seat of enzymic activity. Hulme (1946) has arrived at the latter conclusion.

The fact that phenolic substrates were rapidly oxidized by cut apple tissue immersed in media of pH 3.6–3.7 indicates that polyphenolase was still functioning in the tissues, and provides further support for the theory that *in vivo* the pH of the cytoplasm of the apple was much higher than that of the cell sap.

The volume of enzyme extract obtained from one apple was approximately 7 ml. At $25^{\circ}C$., in the presence of excess substrate and at pH 7.4, this volume of extract was capable of bringing about the uptake of 295 mm.³ of oxygen per 15 minutes, or 1,180 mm.³ per hour; 1,180 mm.³ of oxygen per hour are equal to 1.7 mg. per hour.

This figure is of the same order as the average oxygen uptake per fruit of whole apples respiring at 25°C. Thus, if the pH at the seat of respiration had been in the vicinity of 7.4, the whole of the oxygen uptake of the fruit could have been carried on through the agency of the polyphenolase system. Data to be published shortly indicate that ascorbic acid oxidase may also be of importance in the respiratory metabolism of the apple. There are probably two terminal oxidases, namely, polyphenolase and ascorbic acid oxidase, concerned in the ultimate oxidation of hydrogen by molecular oxygen in this fruit.

SUMMARY.

The effects of protocatechuic acid and other phenolic substances on the respiratory metabolism of cut apple tissue have been studied. Addition of protocatechuic acid to the tissue resulted in an increase in the rate of uptake of oxygen, sometimes accompanied by an increase in the rate of output of carbon dioxide.

Flesh from some of the immature apples treated with protocatechuic acid took up much more oxygen than was necessary for the oxidation of the amount of protocatechuic acid supplied. This indicated that protocatechuic acid was capable of acting as a respiratory catalyst under some conditions.

The respiration of cut apple tissue was strongly inhibited by resorcinol and by 10^{-2} M potassium cyanide.

A crude preparation of polyphenolase was made from Granny Smith apples, using the method of Kubowitz, with slight modifications. The specific activity of this preparation, $W = \frac{\text{mm.}^3 \text{ oxygen taken up}}{\text{mg. dry wt. enz.} \times \text{time (min.)}}$, was approximately equal to 1.4.

The activity of the enzyme preparation towards catechol, protocatechuic acid and p-cresol was studied. Michaelis constants for the complexes formed by the enzyme with catechol, protocatechuic acid and p-cresol respectively were determined. Although the affinity of the enzyme for protocatechuic acid and for p-cresol was found to be about 28 times as great as its affinity for catechol, catechol was oxidized much faster than either protocatechuic acid or p-cresol.

The activity of the enzyme preparation was strongly inhibited by resorcinol and by 10^{-2} M potassium cyanide. Analysis of the data obtained when a given concentration of resorcinol was added to polyphenolase in the presence of various concentrations of substrate showed that resorcinol was acting as a competitive inhibitor. The affinity of the enzyme for resorcinol was very much greater than its affinity for catechol.

The data presented have been discussed in detail, with special reference to the probable importance of polyphenolase as a respiratory enzyme in apples.

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STUDIES IN THE METABOLISM OF APPLES.

VIII. ASCORBIC ACID OXIDASE IN APPLES.

By FRANCES M. V. HACKNEY, M.Sc.

(Six Text-figures.)

[Read 24th November, 1948.]

INTRODUCTION.

The possible importance of ascorbic acid oxidase in the respiratory metabolism of plants has been the subject of investigations by various workers. In 1931 Szent-Gyorgyi isolated a powerful enzyme from cabbage leaves which oxidized ascorbic acid (at that time known as hexuronic acid) with great rapidity. Szent-Gyorgyi named this enzyme "hexoxidase", but it is now known as ascorbic acid oxidase.

Ascorbic acid oxidase has since been isolated from a variety of plant tissues, including Hubbard squash (Tauber, Kleiner and Mishkind, 1935), cabbage, cucumber, cauliflower and marrow (Johnson and Zilva, 1937*a*), bananas, lettuce, string beans and spinach (Stone, 1937). Its oxidizing action on ascorbic acid must not be confused with that of polyphenolase. Ascorbic acid oxidase effects a direct oxidation of ascorbic acid, whereas polyphenolase effects a secondary oxidation by means of the quinones produced during its oxidation of phenols; ascorbic acid oxidase will therefore oxidise ascorbic acid in the absence of any other substance, whereas polyphenolase is incapable of oxidizing ascorbic acid in the absence of suitable phenolic substrate.

In the oxidation of l-ascorbic acid by the oxidase an atom of oxygen and a molecule of water are taken up and dehydro-(oxidized) ascorbic acid is produced. It is an interesting fact that, of the eight isomeric ascorbic acids (namely, l- and d-ascorbic, d- and l-arabo-ascorbic, l- and d-gluco-ascorbic, and l- and d-galacto-ascorbic acids), the oxidase attacks only those enantiomorphs which have some antiscorbutic activity in animals (see Johnson and Zilva, 1937*b*).

Szent-Gyorgyi (1931) was the first to suggest that ascorbic acid might act as a hydrogen carrier in the respiratory metabolism of cabbage. The main objection to this view at the time of Szent-Gyorgyi's work was that no suitable system for the regeneration of reduced ascorbic acid from the dehydro-ascorbic acid could be demonstrated in plant tissues. However, in 1936 Hopkins and Morgan discovered that glutathione, a substance commonly found in plant tissues, was capable of reducing dehydro-ascorbic acid, and suggested that this reduction might play an important part in the respiratory metabolism of plants. More recently, James and Cragg (1943), James, Heard and James (1944), and Bukin (1944) have brought forward evidence of the importance of the ascorbic acid-ascorbic acid oxidase system in the respiratory metabolism of plants. The work of these writers will be discussed in detail in a later section of the paper.

When l-ascorbic acid was added to the media surrounding flesh from Granny Smith apples, evidences of a catalytic effect on respiration were observed. These observations will be described in the present paper.

Johnson and Zilva (1937*a*) considered that ascorbic acid oxidase was not present in apples, and attributed the oxidation of ascorbic acid which they observed with apple juice to the activity of the polyphenolase present in the juice. The writer has observed ascorbic acid oxidase activity in filtered apple juice in the absence of polyphenolase activity. This observation led to the isolation of ascorbic acid oxidase from several varieties of apples. Some of the properties of this enzyme preparation have been studied and will be described.

MATERIALS AND METHODS.

The apples used were similar to those used in the preceding paper of this series. Most of the fruits were immature and mature Granny Smiths of the 1945 and 1946 seasons obtained from a selected orchard at Orange, N.S.W. The mature fruits were part of the mid-April (commercial) picking and were placed in cool store (1°C.) within a few days of harvesting. Samples were withdrawn from store as required and placed in a room maintained at 25°C., at which temperature all subsequent work was carried out. Immature fruits were placed at 25°C. without previous cool storage.

In the earliest experiments fruits of the 1944 season were used. These had been in cool store for 4-5 months.

The Warburg technique described in preceding papers (Studies in the Metabolism of Apples. VI and VII) was used in the investigation of the effects of addition of ascorbic acid to sliced apple tissue.

Ascorbic acid oxidase was extracted from fresh apple juice using the method of Szent-Gyorgyi (1931), with slight modifications. Apple tissue (skin and flesh) was frozen and the juice was extracted by squeezing through muslin; impurities were removed by precipitation with M barium acetate (2 ml. to every 100 ml. juice) and the excess barium acetate was removed by precipitation with 4 ml. saturated ammonium sulphate. These precipitates were discarded. The ascorbic oxidase was then separated out from the supernatant liquid by saturation with ammonium sulphate. It was centrifuged for ten minutes at 2,500 rev./minute, and collected as a layer of scum over a clear supernatant liquid. The precipitate from 100 ml. of apple juice was dissolved in 50 ml. of M/15 phosphate buffer at pH 6.0 and stored in a refrigerator. All steps in the preparation of the enzyme were carried out at room temperature.

Glass distilled water was used in all work described in this paper, and contact of the enzyme preparation with metallic apparatus was avoided. This was done in order to avoid risk of non-enzymic oxidation of ascorbic acid by traces of inorganic copper in the water.

It was found that the enzyme preparation maintained its activity longer when dissolved in phosphate buffer than when dissolved in acetate buffer.

Attempts to isolate ascorbic acid oxidase from apples using the method of Tauber, Kleiner and Mishkind (1935) have so far been unsuccessful.

EXPERIMENTAL RESULTS.

(A). *With Cut Tissue.*

The following notation is used throughout this section:

QO_2 = rate of uptake of oxygen (mm.³/gm./hr.).

QCO_2 = rate of output of carbon dioxide (units as above).

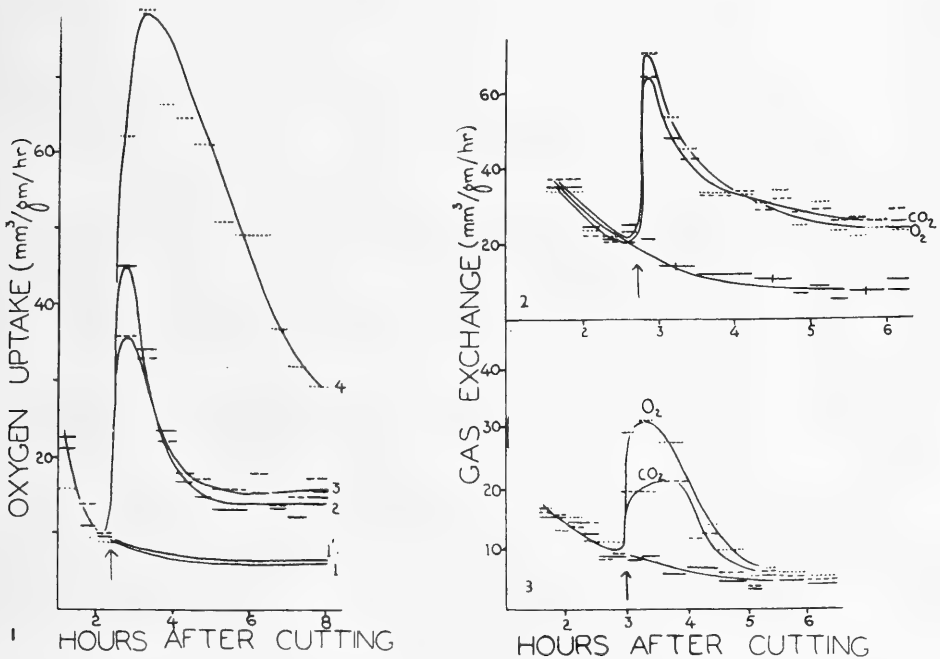
R.Q. = respiratory quotient, or ratio QCO_2/QO_2 .

EFFECTS OF ADDITION OF ASCORBIC ACID TO CUT APPLE TISSUE.

Addition of ascorbic acid (at concentrations of 0.0005 M or more) to the medium surrounding flesh tissue invariably brought about a rise in QO_2 ; addition of ascorbic acid to the medium surrounding cut skin did not bring about any increase in the QO_2 .

Behaviour of Senescent Fruits of the 1944 Season: The QCO_2 was not determined in the experiments carried out on fruits of the 1944 season. Text-figure 1 shows the effects of various concentrations of ascorbic acid on the QO_2 of flesh from senescent apples of the 1944 season. After addition of ascorbic acid to the medium, the QO_2 increased rapidly to a maximum value, the magnitude of which varied according to the concentration of ascorbic acid added. The QO_2 was maintained at the maximum value for a short time only, after which it fell slowly towards the original level. When the logarithm of the rate of excess oxygen uptake (i.e., excess above control level) was plotted against time after treatment a straight line was obtained. The fall in the respiration-time curve after the attainment of the maximum value was therefore exponential; it was probably due to the decrease in substrate concentration which followed upon the oxidation of the

added ascorbic acid. When the concentration of ascorbic acid supplied was high (0.01 M or 0.005 M) the QO_2 was still very much greater than the control value five hours after treatment. When the concentration of ascorbic acid supplied was low (0.001 M or 0.0005 M) the QO_2 rose to its maximum value then fell during the first two hours after treatment, after which it remained at an approximately steady level more than 100% higher than the control level during the remainder of the period of observation (see Text-fig. 1). The values for QO_2 were still greater for the treated tissue than for the control tissue when the experiment was concluded. The total amount of extra oxygen taken up by tissue supplied with 0.44 mg. of ascorbic acid (5 ml. of 0.0005 M solution) was at least 100% greater than the theoretical amount (about 50 mm.³)



Text-figures 1-3.

Figure 1.—The effects of various concentrations of ascorbic acid on the QO_2 of flesh from senescent apples of the 1944 season. Concentrations supplied were 0.0005 M, 0.001 M and 0.005 M, and their effects are shown by curves 2, 3 and 4 respectively; curve 1 shows the behaviour of control (untreated) tissue; curve 1' shows the behaviour of tissue treated with a concentration of ascorbic acid less than 0.0003 M.

Figure 2.—Respiratory behaviour of flesh from very immature apples of the 1945 season in the presence of 0.0005 M ascorbic acid. (Upper set of curves.)

Figure 3.—Respiratory behaviour of flesh from immature apples slightly older than those referred to above, in presence of 0.0005 M ascorbic acid. (Lower set of curves.)

required to oxidize all the acid added (see Text-fig. 1). This result was obtained in several different experiments using senescent fruits of the 1944 season. Its implications will be discussed in a later section. QCO_2 was not measured in the experiments carried out during 1944.

Behaviour of Fruits of the 1945 and 1946 Seasons.

(1) *Immature Fruits.*—When flesh tissue from very immature fruits of the 1945 season (average diameter 2") was supplied with 0.0005 M ascorbic acid it was found that both QO_2 and QCO_2 rose rapidly to a peak value then declined slowly to reach an apparently steady level much higher than that of untreated tissue. The R.Q. was close to unity throughout the experiment. Text-figure 2 shows the respiratory behaviour of one such set of tissue. The total amount of extra oxygen taken up by the tissue during the

first five hours after addition of 0.44 mg. of ascorbic acid was approximately equal to 125 mm.³; this was much greater than the theoretical amount (approximately 50 mm.³) required for the oxidation of the substrate added.

As the apples of the 1945 season advanced in maturity, changes were observed in the behaviour of flesh tissue towards added ascorbic acid. Both QO_2 and QCO_2 rose to peak values after addition of ascorbic acid, but the control levels were regained within two hours after treatment. The amount of extra oxygen taken up by tissue treated with 0.0005 M ascorbic acid was only slightly greater than the theoretical amount required for the oxidation of the substrate added. The R.Q. was less than unity during the first two hours after treatment (see Text-fig. 3).

The behaviour of immature apples of the 1946 season differed in some respects from that of immature apples of the 1945 season. Addition of ascorbic acid to flesh of immature apples of the 1946 season caused a transient rise in QO_2 , with or without a similar rise in QCO_2 . The prolonged effects observed in 1945 were not evident in 1946.

(2) *Mature Fruits*.—The behaviour of flesh tissue from apples of commercial maturity differed from that of flesh tissue from immature apples. Addition of ascorbic acid in any concentration caused a rise in QO_2 but no rise in QCO_2 . The total extra oxygen taken up by treated tissue was no greater than the theoretical amount required for the oxidation of the substrate added.

EXPERIMENTAL RESULTS.

(B). PROPERTIES OF THE ENZYME PREPARATION.

A crude preparation of ascorbic acid oxidase was made from mature Granny Smith apples of the 1946 season. Ascorbic acid oxidase was also isolated from Delicious, Jonathan and Cox's Orange Pippin apples; the preparation from Granny Smith apples was the only one whose properties were studied in detail.

The yields of crude enzyme preparation were of the order of 1 milligram of dry precipitate per gramme of fresh tissue. At pH 5.9 and 25°C. the specific activity of the first preparations towards ascorbic acid,

$$W = \frac{\text{mm.}^3 \text{ oxygen taken up}}{\text{dry wt. enz. (mg.)} \times \text{time (min.)}}$$

was approximately equal to 0.02. This figure was obtained with preparations from fruits removed from store early in June; when more detailed work was done later in the year, it was found that the optimum pH for the enzyme preparation was about 5.2. For preparations made from apples removed from store late in November, W was approximately equal to 0.03, at pH 5.2 and 25°C.

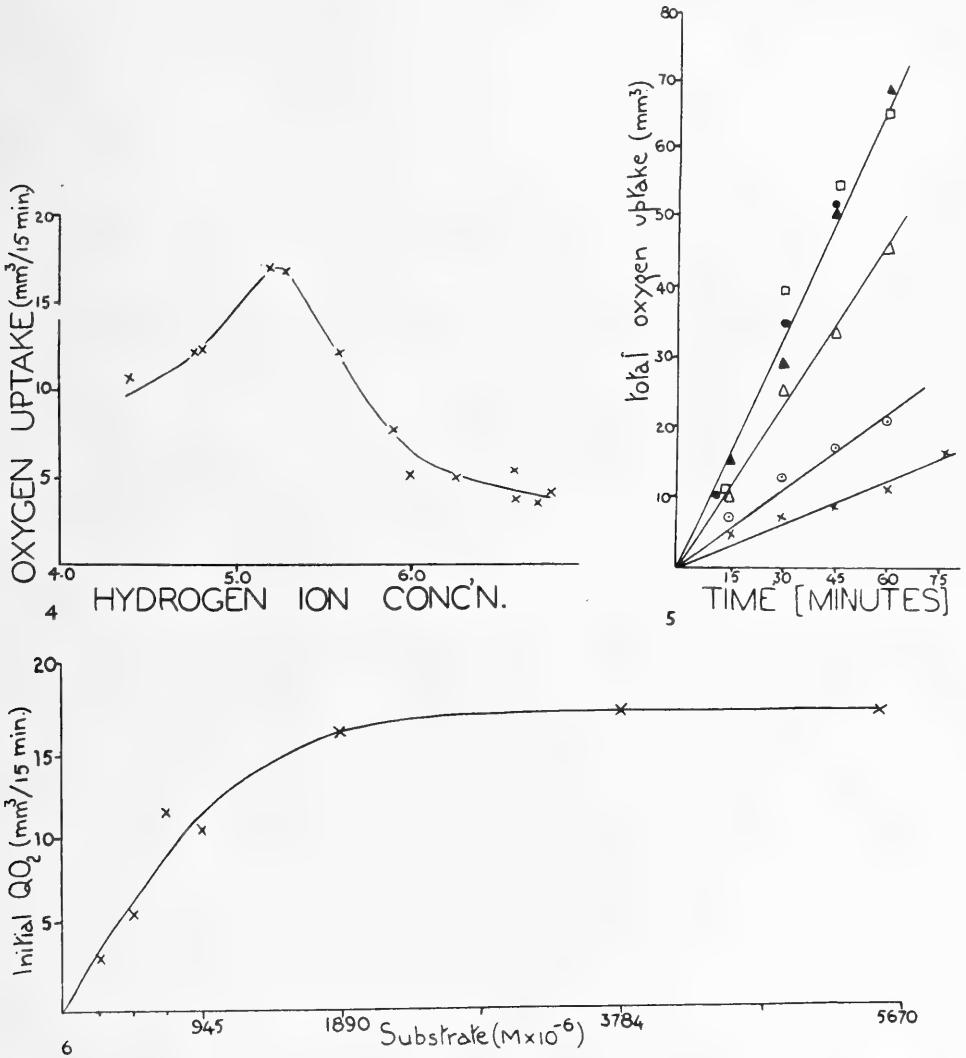
The enzyme preparation had no phenolase activity. This indicates that the oxidation of the ascorbic acid was not due to polyphenolase activity.

The activity of the enzyme preparation was almost completely destroyed by boiling for a few minutes. This indicates that the activity was due to the agency of a protein and not to the presence of inorganic copper. It is a well-known fact that the presence of inorganic copper can be responsible for the oxidation of ascorbic acid in solution. As has already been mentioned, glass-distilled water was used in these experiments in order to avoid inaccuracies due to the presence of traces of copper.

Activity of the Enzyme Preparation Towards Ascorbic Acid: For detailed studies the enzyme preparation was used in M/15 phosphate buffer at pH 5.2; it showed no appreciable uptake of oxygen in the absence of added ascorbic acid. Upon addition of ascorbic acid (neutralized with dilute sodium hydroxide) rapid uptake of oxygen proceeded until all the substrate had been oxidized.

Sensitivity to Potassium Cyanide: The activity of the enzyme preparation was completely inhibited by 10^{-3} M potassium cyanide, at high and low hydrogen ion concentrations. In this it resembled the ascorbic acid oxidase isolated from the Drumstick Tree (*Moringa pterygosperma*) by Srinavasan (1936) rather than that isolated from cabbage by Szent-Gyorgyi (1931).

Effects of Changes in Hydrogen Ion Concentration on the Activity of the Enzyme Preparation: The enzyme preparation was sensitive to changes in the pH of the medium. The activity of 0.5 ml. of enzyme preparation towards ascorbic acid was determined at 25°C. in buffers having a pH range from 4.4 to 6.8 inclusive. Acetate buffers were used for the lower part of the range (up to 5.2 units); phosphate buffers were used from



Text-figures 4-6.

Figure 4.—Activity of ascorbic acid oxidase towards 2 mg. ascorbic acid in buffers of various pH.

Figure 5.—The activity of 0.5 ml. of ascorbic acid oxidase preparation towards various amounts of added ascorbic acid. Concentrations used are the six lowest concentrations used in Figure 6.

Figure 6.—Initial velocity of oxygen uptake by the system ascorbic acid-ascorbic oxidase in the presence of various concentrations of substrate.

5.2 units upwards. There was close agreement between values for activity at pH 5.2 in acetate and in phosphate. Text-figure 4 shows the initial activity of the enzyme towards 2 mg. of ascorbic acid in buffers of various pH. The optimum pH was found to be 5.2-5.3 units. Activity decreased as the pH of the medium increased towards 7.0. Above 7.0 there was rapid autoxidation of the substrate. Control sets without enzyme showed very little autoxidation below pH 7.0.

Effect of Varying the Substrate Concentration: Text-figure 5 shows the activity of 0.5 ml. of enzyme preparation towards various amounts of added ascorbic acid. Text-figure 6 shows the initial velocity of oxygen uptake as a function of substrate concentration. There was an approximately linear relationship between substrate concentration and initial velocity of oxygen uptake for concentrations of ascorbic acid less than 800×10^{-6} M. The maximum rate of oxygen uptake was reached at a concentration of approximately 28×10^{-4} M.

The Michaelis Constant and the Affinity of the Enzyme Preparation for Ascorbic Acid: When the data shown in Text-figures 5 and 6 were analysed by the method of Lineweaver and Burk (1934), the $1/s : 1/v$ plot approximated to the straight line having slope (Km/V) equal to 37×10^{-6} and ordinate intercept (1/V) equal to 0.059. From these values, Km, the Michaelis constant of the enzyme-substrate complex, was calculated as 0.00063 and the maximum velocity, V, was found to be 17 mm.³/15 min. These values agreed well with those obtained by the method of Michaelis and Menten (1913), where Km is taken to be the substrate concentration at which a velocity of reaction equal to half the maximum velocity (obtained by observation) is attained (see Table 1).

TABLE I.
Michaelis Constants and Maximum Velocities of Reaction for Ascorbic Acid Oxidase from Apples; pH 5.2, 25° C.

	Method of L. and B.	Method of M. and M.
Km.	0.00063	0.0006
V.	17.0	16.0

The affinity of the enzyme for ascorbic acid (1/Km) was approximately equal to 1600.

GENERAL DISCUSSION.

Discussion of Behaviour of Tissues Treated with Ascorbic Acid: The behaviour of flesh from very senescent apples of the 1944 season and from very immature apples of the 1945 season suggested that ascorbic acid was acting as a respiratory catalyst. Both QO_2 and QCO_2 were increased by the addition of low concentrations of ascorbic acid to the tissues, and much more oxygen was taken up than was necessary for the oxidation of the amount of acid added. This is the first record of such effects with ascorbic acid.

Boswell (1945) found that addition of ascorbic acid to sliced potato tissue brought about a rise in QO_2 ; this was followed by a fall to the pre-treatment level an hour after treatment. The excess QO_2 was only of the same order as the amount of oxygen required for the oxidation of the ascorbic acid added. Mommaerts (1943), also working with potato tuber, found that addition of ascorbic acid brought about a temporary increase in QO_2 , which was no greater than was necessary for the oxidation of the added ascorbic acid. No ascorbic acid was present in the resting potato tuber. Mommaerts concluded that all the experimental evidence pointed against the hypothesis that ascorbic acid acted as a respiratory catalyst in the resting potato tuber.

The absence of any change in the QO_2 or QCO_2 of apple skin after addition of ascorbic acid could have been due to any one of three reasons:

- (a) Ascorbic acid might have played no part in the respiratory metabolism of the skin;
- (b) there might have been so great an excess of ascorbic acid naturally present in the cells of the skin that the addition of more did not affect the respiration rate (i.e., some factor other than concentration of ascorbic acid was limiting the respiration rate of the skin); or
- (c) the membranes of the cells of the skin might have been impermeable to ascorbic acid.

Dr. F. E. Huelin, Council for Scientific and Industrial Research, Homebush, N.S.W., carried out determinations of ascorbic acid concentration in skin and flesh of mature Granny Smith apples of the 1945 season. The samples taken for analysis were comparable in age and history with those used for determinations of tissue respiration rates by the writer.

A unit of twenty-five apples was selected from a number of cases in which the apples had been uniformly distributed. A one-eighth segment of each apple was taken and peeled thinly with a razor, the skin being dropped into a weighed beaker of 3% metaphosphoric acid. The outer layer of each segment was removed and a thin slice from the freshly-cut surface was dropped into another weighed beaker of 3% metaphosphoric acid. The samples were blended in a Waring blender, made up to 200 ml. and centrifuged. An aliquot sample was taken for titration. The results of the analyses are set out in Table 2.

TABLE 2.
Amount of Ascorbic Acid Present in Samples of Skin and Flesh from Granny Smith Apples after Storage at 1° C.

Date of Removal from Store.	Ascorbic Acid. (Mg./100 gm. fr. wt.)		Percentage Loss.	
	Skin.	Flesh.	Skin.	Flesh.
3. 5.45	132.0	5.9	—	—
5. 6.45	104.6	4.7	20.8	21.3
3. 7.45	83.1	4.1	37.0	30.6
3. 8.45	76.5	4.1	42.0	31.1
3. 9.45	81.4	4.4	30.8	26.0
2.10.45	76.5	3.5	42.0	41.2
6.11.45	63.2	3.6	52.1	38.7
3 12.45	60.7	3.2	54.0	45.4
4. 1.46	64.1	3.5	53.0	41.2

From the above figures it is clear that there was approximately 20–25 times as much ascorbic acid in the skin as in the flesh. Zilva, Kidd and West (1934) had previously found that the ascorbic acid content of Bramley's Seedling apples was highest near the skin. As there were approximately twenty-five times the number of cells per unit weight in the skin of Granny Smith apples as in the flesh (see Hackney, 1945), the amount of ascorbic acid per cell was approximately the same for skin as for flesh. The mean concentration of ascorbic acid per unit fresh weight was, however, much greater in the skin than in the flesh (0.008 M as compared with 0.0003 M, in the first sample). The addition of 0.01 M ascorbic acid (the highest concentration used in 1945 and 1946) might, therefore, have been expected to bring about a greater effect in the flesh than in the skin. It is interesting to note that the lowest effective concentration of ascorbic acid added to the flesh (0.0005 M) was only slightly higher than the mean concentration naturally present per unit fresh weight of flesh (0.0003 M). When skin from very senescent apples of the 1946 season was treated with 0.03 M ascorbic acid on 8.1.47, no effect on QO_2 was observed. When flesh from the same apples was treated with ascorbic acid a rise in QO_2 was observed. It is possible that the skin is less permeable than the flesh to ascorbic acid. Boswell (1945) considered that very little of the ascorbic acid added to potato tissue entered the cells.

It is clear from Table 2 that there was a marked decrease in the amount of ascorbic acid present in both skin and flesh during storage at 1°C. The rate of percentage loss of ascorbic acid was accelerated during the storage life. The percentage decrease in ascorbic acid content was of the same order in the skin as in the flesh, so that the

ratio of the concentration in the skin to the concentration in the flesh remained approximately constant throughout the storage life. Zilva, Kidd and West (1933) determined the ascorbic acid content of Bramley's Seedling apples during development. They found that the total quantity of ascorbic acid per unit fresh weight remained constant throughout development, but that there was a change in the relative proportions of the two forms (oxidized and reduced); the proportion of the reduced form increased and that of the oxidized form decreased as the apple approached maturity.

It is difficult to explain the changes which occurred in the behaviour of flesh tissue towards added ascorbic acid as the apples advanced in maturity. It is possible that in some immature apples there were ample supplies of the substances responsible for the reduction of ascorbic acid, subsequent to its oxidation by the ascorbic acid oxidase. Addition of ascorbic acid to tissue from these apples could bring about catalytic effects. In other immature apples, and in mature apples, the reducing system might have been working as fast as possible prior to treatment with ascorbic acid; the addition of ascorbic acid to tissues from these apples could not bring about catalytic effects, since the main factor limiting respiration rate was concentration of reducing substance, not concentration of ascorbic acid.

Potential Quantitative Activity of Ascorbic Acid Oxidase in Apples: Ascorbic acid oxidase and many other enzymes are incapable of any great activity at the pH of expressed apple juice (3.67). If ascorbic acid oxidase takes part in the respiratory metabolism of the apple, it must be assumed that the pH of the cytoplasm at the seat of enzymic activity is much higher than the pH of the expressed juice.

It was determined experimentally that, at pH 5.3 and 25°C., 22 mg. (dry wt.) of enzyme preparation were capable of consuming 68 mm.³ of oxygen per hour. The average amount of enzyme preparation obtained from a single fruit was about 140 mg. This amount of enzyme could have consumed approximately 420 mm.³ oxygen per hour, or 0.6 mg. per hour. The rate of oxygen uptake of an intact Granny Smith apple was of the order of 1.5 mg. per hour at 25°C. Thus, the amount of ascorbic acid oxidase extracted from an apple was capable, under optimum conditions of pH and substrate supply, of carrying out a little more than one-third of the oxygen uptake by the fruit. This is a conservative estimate of the capacity of the enzyme *in vivo*, since no allowance has been made for loss of activity during extraction, and it has been assumed that all the enzyme in the apple is included in the extract.

It has already been shown (Hackney, these PROCEEDINGS, 1948, p. 439) that there is sufficient polyphenolase present in the Granny Smith apple to cope with all the oxygen uptake by the fruit, under certain conditions of hydrogen ion concentration. There is therefore more than enough ascorbic acid oxidase plus polyphenolase to account for all the oxygen uptake.

At present it appears that there are two terminal oxidases active in the respiratory metabolism of the apple—polyphenolase and ascorbic acid oxidase. Cytochrome oxidase is probably absent from apples (Hackney, *op. cit.*).

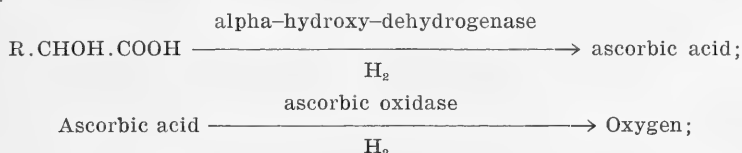
The Rôle of Ascorbic Acid Oxidase in Respiration: Although the biological importance of ascorbic acid has long been recognized, its function or functions in the metabolism of plant and animal cells is not known. In 1934 Quastel and Wheatley found that addition of ascorbic acid to rat liver slices in certain media brought about a prolongation of the steady rate of oxygen uptake. In glycerophosphate-Locke medium, containing sodium butyrate or crotonate, the production of acetoacetate was enhanced by the presence of ascorbic acid. Quastel and Wheatley suggested that this was due to the rate of oxidation of fatty acids being inherently connected with the rate of respiration. In 1944 Tien Ho Lan and Sealock found that liver or kidney slices from scorbutic guinea pigs did not possess the normal ability to metabolize tyrosine. When ascorbic acid was added to such tissue, the ability to metabolize tyrosine was regained. A link between ascorbic acid metabolism and tyrosine metabolism was thereby indicated.

When ascorbic acid and protocatechuic acid were added simultaneously to apple flesh by the writer, the extra oxygen taken up was approximately equal to the sum of the extra QO_2 s observed when the two substances were added separately. This seemed to indicate that the two substances were oxidized by independent mechanisms (see Krebs, 1943). In two experiments carried out by the writer the extra QCO_2 after addition of ascorbic acid plus catechuic acid was greater than the sum of the extra QCO_2 s observed when the two substances were added separately, but this effect was not repeated in subsequent experiments.

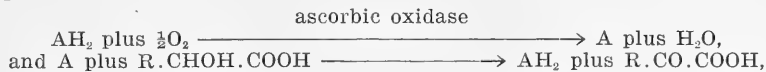
The fact that ascorbic acid oxidase is apparently absent from animal tissue is sufficient to suggest that the rôle of ascorbic acid in animals may be different from its rôle in plants. A good deal of research has recently been carried out regarding the possible rôle of ascorbic acid in plants. It has been postulated by several workers, including Szent-Gyorgyi (1931) that ascorbic acid may play the rôle of terminal oxidase in plant respiration (cf. cytochrome oxidase in animal respiration). The main objection to this view has been the fact that so little was known of the systems which reduce dehydroascorbic acid. The work of Hopkins and Morgan (1936) indicated that reduced glutathione (GSH) might be the principal reducing agent of dehydroascorbic acid *in vivo*.

The latest investigations regarding the rôle of ascorbic acid oxidase in plant respiration include those of James and Cragg (1943), James, Heard and James (1944), and Bukin (1944).

James and Cragg observed the oxidation of ascorbic acid by barley juice extract. They showed that this oxidation was not due to the action of cytochrome oxidase, tyrosinase (polyphenolase) or peroxidase, and must therefore have been due to the action of either ascorbic acid oxidase or some other enzyme hitherto unknown. From their observations of the effects of addition of organic acids (e.g., lactic, glycollic and tartaric acids) which increased the oxygen consumption of their barley extract, James and Cragg concluded that those acids which have an OH group in the alpha position on the molecule (excluding malic acid) may provide the mechanism for the reduction of oxidized ascorbic acid in tissues. They suggested the following mechanism of hydrogen transport:



depending on the reactions,



where A represents ascorbic acid in the oxidized form.

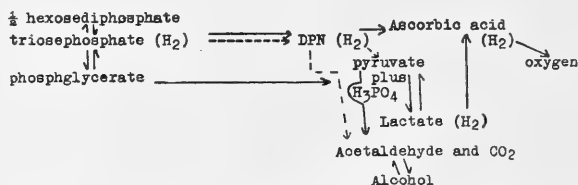
In these reactions James and Cragg were able to observe the following steps:

- (1) The consumption of oxygen and ascorbic acid (AH_2).
- (2) The reduction of oxidized ascorbic acid in the presence of alpha-hydroxy acid.
- (3) The formation of an alpha-keto acid end product.

Reduction of ascorbic acid was most vigorous in the presence of lactic acid, which makes the metabolic status of this acid very interesting; two possibilities are open as regards the rôle of lactic acid in the metabolism of barley:

- (1) Lactic acid may be an intermediate product, continuously being oxidized to pyruvic acid, or
- (2) lactic-pyruvic may act as a redox system, standing in the same relationship to ascorbic acid as the system succinic-fumaric stands to cytochrome.

In later work, James, Heard and James (1944) suggested that barley might decompose hexosediphosphate in the following reactions:

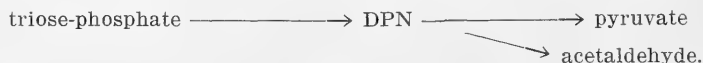


Dotted lines indicate anaerobic transfer of hydrogen, entire lines indicate aerobic transfer.

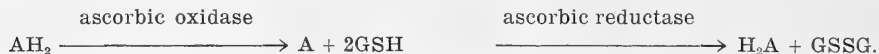
The evidence of a connection between glycolysis and oxidation via ascorbic acid listed by James, Heard and James is as follows:

- (1) Addition of ascorbic acid to barley extract increases loss of hexosediphosphate and gain of the unhydrolysable ester (probably phosphoglycerate).
- (2) Addition of hexosediphosphate only caused an increase in oxygen uptake if ascorbic acid was also added, but it then increased the oxygen uptake much more than when ascorbic acid was added alone.
- (3) The oxygen uptake was considerably accelerated when diphosphopyridine nucleotide (DPN) was added to the system in the presence of ascorbic acid.

James, Heard and James put forward a considerable amount of evidence for the above schema. They consider that when oxygen is present the normal course of hydrogen transfer is probably triose-phosphate $\xrightarrow{\text{-----}}$ DPN $\xrightarrow{\text{-----}}$ ascorbic acid $\xrightarrow{\text{-----}}$ oxygen; when oxygen and ascorbic acid are absent the course of hydrogen transfer is deflected to the internal hydrogen acceptors:



The latest work available on the rôle of ascorbic acid in plant respiration is an abstract of work by Bukin (1944), who compared the rate of oxygen uptake by intact tissue with the rate of oxidation of ascorbic acid by fermenting pulp, for several different plants. The two rates were found to be of the same order. Bukin considers that a system involving ascorbic acid might enable transmission of all the hydrogen used during respiration. He is of the opinion that cauliflower juice (as used by Szent-Gyorgyi, 1931) contains an enzyme other than ascorbic acid oxidase, which is capable of acting in conjunction with ascorbic acid oxidase to form a system by which two molecules of glutathione (GSH) reduce one molecule of ascorbic acid and return it to the sphere of action:



Ascorbic reductase acts differently from ascorbic oxidase towards heating and cyanide poisoning.

In order to postulate that the above system could take part in the respiratory metabolism, it was necessary to find some substance present in the cells which was capable of reducing GSSG back to GSH with considerable rapidity. It was found that when GSH was added to oxidized ascorbic acid in the presence of DPN, the resultant reduction of the ascorbic acid was much faster than when GSH was added alone. The extent of the acceleration of the reaction was proportional to the amount of DPN added. It was subsequently found that DPN was capable of reducing GSSG with great rapidity; the velocity of the reaction was apparently of the same order as the rate of oxidation of DPN by other hydrogen acceptors, including flavoproteins.

Thus Bukin, and James and his co-workers, have arrived independently at the conclusion that DPN is probably very important in the reduction of ascorbic acid in plant tissues. All the evidence at present available suggests strongly that the system ascorbic acid-ascorbic acid oxidase may constitute an essential part of the respiratory chain in some plants.

The results of the investigations of the effects of addition of ascorbic acid to cut apple tissue indicate that part of the respiratory metabolism of this tissue is probably carried on through the agency of ascorbic acid oxidase. The evidence to hand favours the view that ascorbic acid may function not only in high concentrations as a substrate for its oxidase, but in low concentrations as an important hydrogen carrier in some types of respiration.

ACKNOWLEDGEMENTS.

The writer takes this opportunity of expressing her appreciation and indebtedness to Professor E. Ashby, formerly of the Botany Department, University of Sydney (now of the Botany Department, University of Manchester), for the use of his laboratories and facilities, and for his helpful advice and criticism of this work; also to Professor N. A. Burges, Botany Department, University of Sydney, for his criticism of the manuscript. The writer also wishes to express her thanks to Professor J. S. Turner, Botany Department, University of Melbourne, and to Dr. R. N. Robertson, Council for Scientific and Industrial Research, Homebush, N.S.W., for valuable suggestions regarding the investigation of the respiratory metabolism of cut apple tissue; also to Mr. J. Falk, formerly of the Department of Organic Chemistry, University of Sydney, for his helpful advice regarding the isolation and identification of ascorbic acid oxidase from apples. The writer also acknowledges with gratitude the helpful suggestions kindly made by Dr. F. E. Huelin, Council for Scientific and Industrial Research, during the course of the work.

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ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

26th MAY, 1948.

Dr. Lilian Fraser, President, in the Chair.

The President congratulated Mr. R. H. Wharton on his appointment as entomologist to the Malaria Research Institute of the Federated Malay States.

Donations and Exchanges received since the previous Monthly Meeting (28th April, 1948), amounting to 2 Volumes, 42 Parts or Numbers, 6 Bulletins and 1 Report, total 51, have been added to the Library.

PAPERS READ.

1. Revision of the genus *Brachycome* Cass. Part I. Australian Species. By Gwenda L. Davis, B.Sc.
2. The Anopheline Mosquitoes of North-West Borneo. By D. H. Colless, B.Sc.Agr.

EXHIBITS.

Miss M. Tindale exhibited a herbarium specimen of *Cyathea marcescens* N. A. Wakefield, which was described as a new species in the Victorian Naturalist, Vol. lix, No. 2, 1942. So far this tree-fern has only been recorded from Victoria where it occurs in the Otway Ranges and at Mt. Drummer and Combiobar in East Gippsland.

Mr. L. Johnson exhibited a herbarium specimen of *Chenopodium leptophyllum* (Moq.) S. Wats. collected at Broken Hill. This species is a native of the drier parts of the United States and has not been recorded previously from New South Wales. Although regarded in America as a distinct species, it is probably more correctly regarded as a geographical subspecies of the Eurasian *Chenopodium album* which is a common weed in Australia. Mr. Johnson also exhibited a specimen of *Richardia scabra* L. (Rubiaceae) collected at Cheltenham, where it occurs in association with *R. stellaris* (Cham. et Schlecht) Steud. *R. scabra* or Mexican clover is a native of tropical America and has been recorded previously only from Queensland and the far north coast of New South Wales, where it is a troublesome weed of cultivation.

Dr. Lilian Fraser exhibited a specimen of the custard apple affected with brown rot due to *Phytophthora parasitica*. This is believed to be a new record.

ORDINARY MONTHLY MEETING.

30th JUNE, 1948.

Dr. Lilian Fraser, President, in the Chair.

The President referred to the death of the Rev. E. N. McKie, who had been a member of the Society since 1927, and of Captain J. D. McComish, who had only recently been elected a member.

Miss Mary Besly, Messrs. Roy P. Cooper, Ian M. Fraser and Alan V. Jopling were elected Ordinary Members of the Society.

Donations and Exchanges received since the last Monthly Meeting (26th May, 1948), amounting to 19 Volumes, 109 Parts or Numbers, 2 Bulletins, 3 Reports and 6 Pamphlets, total 139, have been added to the Library.

PAPERS READ.

1. Orchid Flora of the Central Western Slopes of New South Wales. By the Rev. H. M. R. Rupp.
2. The Embryogeny of *Pterosphaera Hookeriana*. By C. G. Elliott. (*Communicated by Professor S. Warren Carey.*)

3. Some Observations on *Myrmecia tarsata* (Smith). By the Rev. J. J. McAreavey. Symposium on "James Stuart and his Paintings".

This symposium was arranged by Messrs. A. Musgrave, G. P. Whitley, T. Iredale and Dr. Frank Marshall. Mr. A. Musgrave gave an outline of the biography of James Stuart, who came to Sydney in 1834; Mr. G. P. Whitley described the fishes drawn by James Stuart; and Mr. T. Iredale described the birds. Some of the original paintings were exhibited and the speakers illustrated their remarks with slides made from the paintings through the interest of Dr. Frank Marshall of the Royal Zoological Society of New South Wales.

ORDINARY MONTHLY MEETING.

28th JULY, 1948.

Dr. Lilian Fraser, President, in the Chair.

The President referred to the death on 1st July of Mr. E. C. Andrews, who had been a member since 1899. The following resolution was passed at the July Council Meeting:

"This Council desires to place on record its sense of the Society's loss in the death of Mr. E. C. Andrews. For many years he served as a member of this Council and for one session as President. He occupied a very high place among scientific workers, and added very considerably to our knowledge, particularly of the geology and physiography of the Commonwealth as well as of the philosophical aspects of geology. In addition, he was an energetic supporter of many organizations for the advancement of Science, which benefited much from his sound judgment and wide experience."

The President offered congratulations to Miss Daphne C. Davison, M.Sc., on the award of an 1851 Exhibition Scholarship.

The President announced that Mrs. Messmer is organizing an excursion to Cradle Mt., Tasmania, to take place after the Hobart Science Congress next January. Those interested should get in touch with Mrs. Messmer, JX 1745.

Miss Dorothy E. Shaw and Messrs. Tom Manefield, Jr., and Robert Smith were elected Ordinary Members of the Society.

Donations and Exchanges received since the last Monthly Meeting (30th June, 1948), amounting to 3 Volumes, 24 Parts or Numbers, 10 Bulletins, 2 Reports and 5 Pamphlets, total 44, have been added to the Library.

NOTES AND EXHIBITS ON AN EXCURSION TO THE GREAT BARRIER REEF. BY MEMBERS OF THE SYDNEY UNIVERSITY BIOLOGICAL SOCIETY.

The talk which dealt with a trip to Heron Island on the Barrier Reef by members of the Sydney University Biological Society in January, 1948, was illustrated by lantern slides, pictures, maps and specimens.

The trip up to the island was described and maps were shown indicating the position of Heron Island in the Capricorn Group. The main types of islands found in the Barrier Reef area were referred to and Heron Island was described as an example of the third type, or Coral Cay. Theories of formation of a Coral Cay were also mentioned.

Methods of collecting on the reef were explained, and tribute was paid to the late Professor Goddard of Brisbane University for his assistance to members of the party during collecting trips. Reasons were given for dividing the beach and reef area into a series of zones to facilitate an ecological survey of the fauna, most of the time being spent on a description of four of the six zones studied, i.e., on the reef area. The remaining two zones, the sandy beach and the rock platform, were only referred to briefly.

The sequence of corals from the shore-line to the edge of the reef was described as well as the distribution of soft corals. Some of the more interesting and colourful inhabitants of the reef were mentioned whilst a little time was spent in referring to some of the animal associations found on the reef. The life-history of the turtle, which was breeding on the island at the time, was described, and reference was made to the occurrence of several species of birds on the island.

The Botany undertaken by the expedition fell into two parts; (a) the floristics and ecology of the island, (b) the Algae from the surrounding reef. Twenty-seven species of Angiosperms were identified and of these the following three are new records for the Bunker-Capricorn group: *Cakile maritima* Scop., *Cenchrus echinatus* L., and *Euphorbia heterophylla* L. Four others had been found previously in the island group but not on Heron Island itself. These are *Celtis paniculata* Planch., *Erigeron unifolius* Willd., *Portulaca oleracea* L., *Salsola kali* L. A detailed study of the ecology of the island was made and the distribution of the important species was mapped. The vegetation could be divided into four zones: (a) marginal zone of grasses, (b) *Casuarina* belt, (c) intermediate zone—the richest floristically, (d) *Pisonia* zone. *Pisonia brunoniana* Endl. is the highest form of vegetation developed on coral sands under these climatic conditions. Factors affecting this zonation were discussed. Analyses of soil samples from each zone were also made. As well as carrying out a study of the Angiosperms, thirty species of Algae were collected. These have been identified by Mrs. V. Jones of the C.S.I.R., who found one species, *Caulerpa anceps* Harv., which has not previously been recorded from Australia, and two other quite rare species, *Gelidiopsis intricata* (Ag.) Vickers and *Gelidiella acerosa* (Forst.) Feldmann and Hamel.

ORDINARY MONTHLY MEETING.

25th AUGUST, 1948.

Dr. Lilian Fraser, President, in the Chair.

The President referred to the death of Mr. M. S. Barnett, who had been a member of the Society since 1919.

Donations and Exchanges received since the last Monthly Meeting (28th July, 1948), and amounting to 25 Volumes, 115 Parts or Numbers, 11 Bulletins and 2 Reports, total 153, have been added to the Library.

Miss J. Vickery gave a talk on the Royal Botanic Gardens, Kew, and its link with the history of botany and the botanical exploration of Australia. She briefly traced the history of the Gardens from the time when they were the domains attached to Royal residences, and from the small botanic garden commenced by the Princess Dowager of Wales in 1759 up to the present day. They now cover an area of 288 acres and attract a few millions of visitors each year. Their existence, however, has depended more upon the inconspicuous work which the institution has performed in the study and development of empire resources, and its encouragement of botanical exploration and provision of knowledge regarding colonial floras. The zeal and wisdom of the early directors and associated botanists attracted correspondents from all over the world, who sought their advice and assistance on innumerable problems. Amongst correspondence preserved in the Library are letters from many Australian botanists and horticulturalists. Many of these are of considerable historical interest, and extracts from a few were read in illustration of the light which they may sometimes throw on the affairs of the last century.

The Herbarium is rich in type specimens of Australian plants, and contains also the majority of the specimens studied by Bentham in the preparation of the *Flora Australiensis*, the chief comprehensive pioneer work on Australian botany.

A series of colour photographs illustrative of some aspects of the Kew Gardens was shown, including the rock garden, the gardens along the Broad Walk, the glasshouse and the water gardens.

The Secretary gave a brief talk on several Western Australian minerals. These included glauconite (a hydrous silicate of iron and potassium) which occurs as a main constituent in the Cretaceous greensands at Gingin and from which a water-softener is manufactured; alunite (a hydrous sulphate of aluminium and potassium) from Chandler which is now being worked for the production of potassium salts; beryl (beryllium aluminium silicate) and tantalite (tantalate and niobate of iron and manganese). The two latter minerals were produced during the war as essential minerals of great strategic importance.

ORDINARY MONTHLY MEETING.

29th SEPTEMBER, 1948.

Dr. Lilian Fraser, President, in the Chair.

Mr. James A. Keast was elected an Ordinary Member 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, 1949, from qualified candidates. Applications should be lodged with the Secretary not later than Wednesday, 3rd November, 1948.

Donations and Exchanges received since the last Monthly Meeting (25th August, 1948), amounting to 9 Volumes, 53 Parts or Numbers, 2 Bulletins, and 13 Pamphlets, total 77, have been added to the Library.

PAPERS READ.

1. Preliminary Studies on the Ascigerous Stage of *Phoma citricarpa* McAlp., and its Relation to Black Spot of Citrus. By Temple B. Kiely.

2. Studies on Australian Marine Algae. IV. Further Geographical Notes. By Valerie May.

3. Miscellaneous Notes on Australian Diptera. XIV. Venation and other Notes. By G. H. Hardy.

4. Diptera of the Territory of New Guinea. XIV. Family Tabanidae. Part iii. Tabaninae. By H. Oldroyd. (*Communicated by Dr. G. A. M. Heydon.*)

NOTES AND EXHIBITS.

Miss M. Tindale exhibited a specimen of *Acacia Muelleriana* J. H. Maiden and R. T. Baker obtained by Mr. E. F. Constable at Cox's Gap, near Muswellbrook, N.S.W. This species was described in the PROC. LINN. SOC. N.S.W., Sec. Series (VIII) (1893), 515. The holotype was collected by J. Dawson in the Upper Hunter River district at the foot of the ranges. *A. Muelleriana* has a very restricted distribution, as it occurs only on the north-western slopes and central-western slopes of New South Wales. Specimens from Goonoo, Minore, Dubbo, Talooobie, Murrumbo and Mudgee are located in the National Herbarium, Sydney. This wattle is a member of the *Acacia decurrens-mollissima* group. The ultimate segments are from 1 to 2 cm. in length and are much longer than in most members of this group. This species is usually a shrub or small tree up to 20 ft. in height. So far it is unimportant in the tanning-bark industry.

Miss R. Curtis exhibited test plants which had been treated with different concentrations of hormone, this being the final stage in the *Avena colyptile* test. The interest of this test is that biological material is used to measure very small differences in concentration of hormone. The conditions in which the plants are grown and treated are strictly controlled with respect to temperature, humidity and light.

ORDINARY MONTHLY MEETING.

27th OCTOBER, 1948.

Dr. Lilian Fraser, President, in the Chair.

Miss Ruth Wolf, B.Sc., was elected an Ordinary Member 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, 1949, from qualified candidates. Applications should be lodged with the Secretary not later than Wednesday, 3rd November, 1948.

Donations and Exchanges received since the last Monthly Meeting (29th September, 1948), amounting to 15 Volumes, 51 Parts or Numbers, 1 Report, 7 Pamphlets, total 74, have been added to the Library.

PAPERS READ.

1. Taxonomic Notes on the Genus *Ablepharus* (Sauria: Scincidae). II. The Races of *Ablepharus burnetti* Oudemans. By S. J. Copland.
2. Revisional Notes on Australasian Simuliidae (Diptera). By I. M. and M. J. Mackerras.
3. New Species of Simuliidae from New South Wales. By R. H. Wharton.
4. Observations on the Comparative Survival of various Stages of *Aedes (Stegomyia) scutellaris* Walker and *Aedes (Stegomyia) aegypti* Linnaeus at varying Temperatures and Humidities. By A. R. Woodhill.
5. Bryozoa from the Upper Carboniferous of Queensland and New South Wales. By Joan Crockford.

ORDINARY MONTHLY MEETING.

24th NOVEMBER, 1948.

Dr. Lilian Fraser, President, in the Chair.

The President announced that Linnean Macleay Fellowships had been awarded for 1949 to: Miss Muriel Morris, B.Sc. (reappointment in Zoology); Miss Judith Balmain, B.Sc. (Biochemistry); Miss Mary Hindmarsh, B.Sc. (Botany), and Miss Adele Millerd, B.Sc. (Biochemistry).

The President referred to the appointment of Professor P. D. F. Murray, a former Linnean Macleay Fellow, to the Chair of Zoology in the University of Sydney.

The President congratulated Miss F. M. V. Hackney on obtaining the degree of D.Sc. of the University of Sydney.

Donations and Exchanges received since the last Monthly Meeting (27th October, 1948), amounting to 1 Volume, 20 Parts or Numbers, 5 Bulletins, 2 Reports and 14 Pamphlets, total 42, have been added to the Library.

PAPERS READ.

1. Studies on Formic Hydrogenlyase in Washed Suspensions of *Escherichia coli*. By June Lascelles.
 2. Studies in the Metabolism of Apples. VII. A Study of the Polyphenolase System in Apples. By Frances M. V. Hackney.
 3. Studies in the Metabolism of Apples. VIII. Ascorbic Acid Oxidase in Apples. By Frances M. V. Hackney.
- Dr. R. N. Robertson gave a talk on "Some Impressions of Botanical Laboratories Abroad".

NOTES AND EXHIBITS.

Mr. C. E. Chadwick exhibited specimens of *Amblypelta nitida* Stål, identified by Mr. A. Musgrave; also photographs and damaged specimens of peaches, plums and nectarines. This bug, green when alive, is a member of the Family Coreidae and was described by Stål in 1873 (*K. svenska VetenskAkad. Handl.*, xi: 75) from Rockhampton, Qld. In 1911 Distant (*Ann. Mag. Nat. Hist.* (8) vii: 531) described *Pendulinus lutescens* from Mackay, Qld. China in 1934 (*Bull. Ent. Res.*, xxv, 2 (July): 188) stated that *P. lutescens* Dist. should be referred to the genus *Amblypelta*. When the descriptions of Stål and Distant were compared with the insect there seemed to be no doubt that they referred to one and the same species, so that the specific name *lutescens* Dist. can only be regarded as a synonym of *nitida* Stål.

Veitch and Simmonds (Pests and Diseases of Queensland Fruits and Vegetables, 1929, p. 114) stated that the insect occurred along the coastal areas of Queensland from Cairns to Brisbane. The Australian Museum has a specimen of a male collected from Byfield in November, 1926, and a female from a grass tree at Eastwood in April, 1940.

Economically the insect is a pest of bananas at Byfield, near Rockhampton. It feeds on the fruit and dark pits develop as a result. Smith (*Qd. Agric. J.*, 1937, xlviii, 5 (November), 554) mentioned the bug under the name of the "fruit-spotting bug" as a pest of papaws, and Sloan (*Qd. Agric. J.*, 1946, lxii, 4 (April), 229-233) dealt more fully with its habits and recorded a number of other host plants. Additional host plants are noted by Brimblecombe in a paper to be published in the *Queensland Agricultural Journal* for October, 1948. The N.S.W. Department of Agriculture has specimens of the insect which were said to be "attacking fruit trees" at Warrawee in December, 1928. Late in October this year specimens were received from Mosman and Turramurra, where they were causing pitting in plums, nectarines and peaches. More recently they were recorded from peaches at Baulkham Hills. Experimental work on the insect is now proceeding at the Department of Agriculture. The shield bug, *Lampromicra aerea* Dist. (Family Pentatomidae) has recently been recorded attacking peaches at Carlingford. The fruit develop an irregular surface, but not the pitting so obvious in the case of *A. nitida* Stål. Likewise, the gum pockets and gummy exudations observed in the case of damage by *A. nitida* Stål have not yet been observed in fruit attacked by this species.

LIST OF PLATES.

PROCEEDINGS, 1948.

- i.—Cytology of the Myrtaceae.
 - ii.—Pollen of the Myrtaceae.
 - iii-iv.—Cytology of the Epacridaceae.
 - v.—Australasian Ceratopogonidae.
 - vi-xiii.—The Genus *Brachycome* Cass.
 - xiv.—Carl Adolph Susasmilch.
 - xv-xxi.—Studies on *Guignardia citricarpa* n.s.
 - xxii.—The Genus *Ablepharus*.
-

LIST OF MEMBERS.

(15th December, 1948.)

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- 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.
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- 1941 Blake, Stanley Thatcher, M.Sc., Botanic Gardens, Brisbane, Queensland.
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- 1923 Brough, Patrick, M.A., D.Sc., B.Sc.Agr., Botany School, Sydney University.
- 1924 Brown, Miss Ida Alison, D.Sc., Department of Geology, Sydney University.
- 1911 Browne, William Rowan, D.Sc., Department of Geology, Sydney University.
- 1947 Browning, T. O., Waite Agricultural Research Institute, Adelaide, South Australia.
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- 1942 Cleland, Kenneth Wollaston, M.B., Department of Anatomy, Sydney University.
- 1931 Colefax, Allen Neville, B.Sc., Department of Zoology, Sydney University.
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- 1928 Craft, Frank Alfred, B.Sc., 10 Bank Street, Wellington, N.S.W.
 1946 Crust, Miss Mabel, B.Sc., 21 Silex Road, Mosman, N.S.W.
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- 1947 Johnson, Lawrence Alexander Sidney, 178 Beecroft Road, Cheltenham, N.S.W.
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- 1909 Walkom, Arthur Bache, D.Sc., Australian Museum, College Street, Sydney.
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 1926 *Whitley, Gilbert Percy, Australian Museum, College Street, Sydney.
 1946 Wilkins, Miss Marjorie Jessie, B.Sc., 33 Muston Street, Mosman, N.S.W.
 1947 Windridge, Mrs. Judith, B.Sc., Department of Geology, Sydney University.
 1947 Winkworth, Robert Ernest, Botany Department, University of Melbourne, Carlton, N.3, Victoria.
 1934 Womersley, Herbert, F.R.E.S., A.L.S., South Australian Museum, Adelaide, South Australia.
 1932 Woodhill, Anthony Reeve, B.Sc.Agr., Department of Zoology, Sydney University.
- 1936 Zeck, Emil Herman, 694 Victoria Road, Ryde, N.S.W.

HONORARY MEMBER.

- 1923 Hill, Professor James Peter, D.Sc., F.R.S.Z., F.Z.S., F.R.S., "Kanimbla", Dollis Avenue, Finchley, London, N.3, England.

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 1943 Waterhouse, Gustavus Athol, D.Sc., B.E., F.R.E.S., c.o. Mrs. Millett, Illoura Avenue, Wahroonga, N.S.W.

* Life Member.

LIST OF GENERA AND SPECIES DESCRIBED AS NEW IN THIS VOLUME
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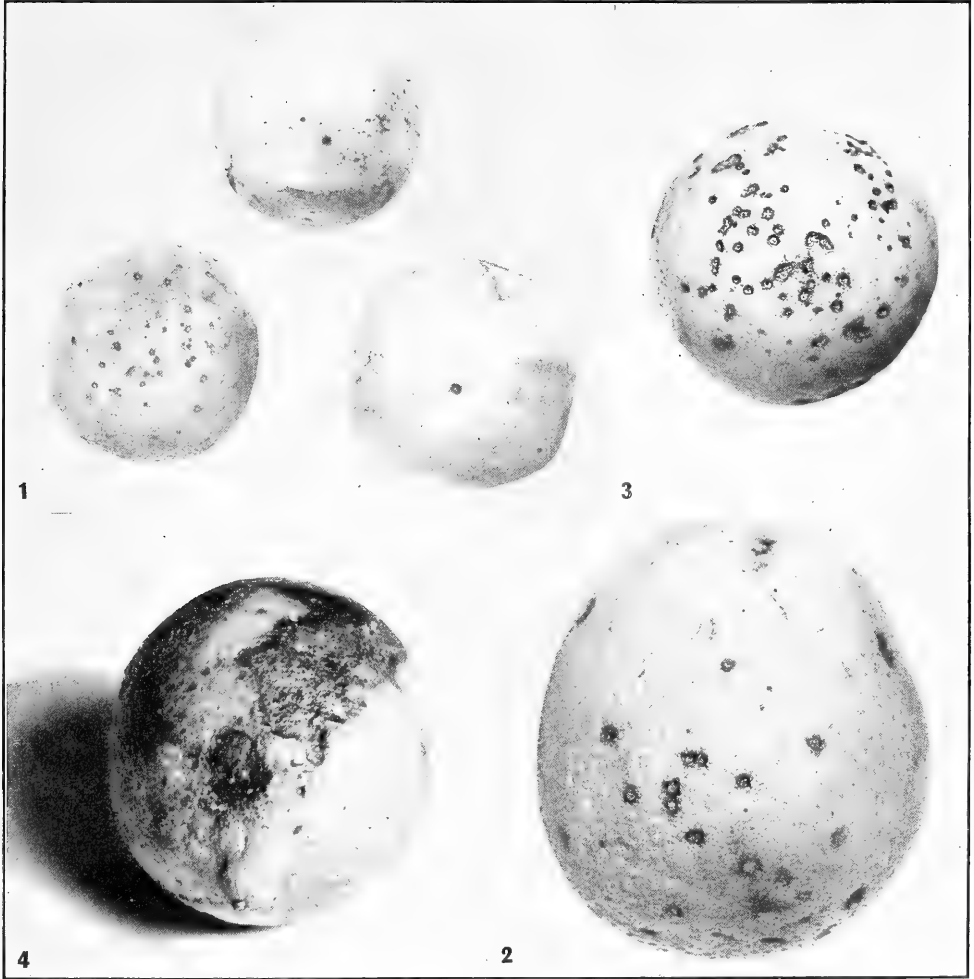
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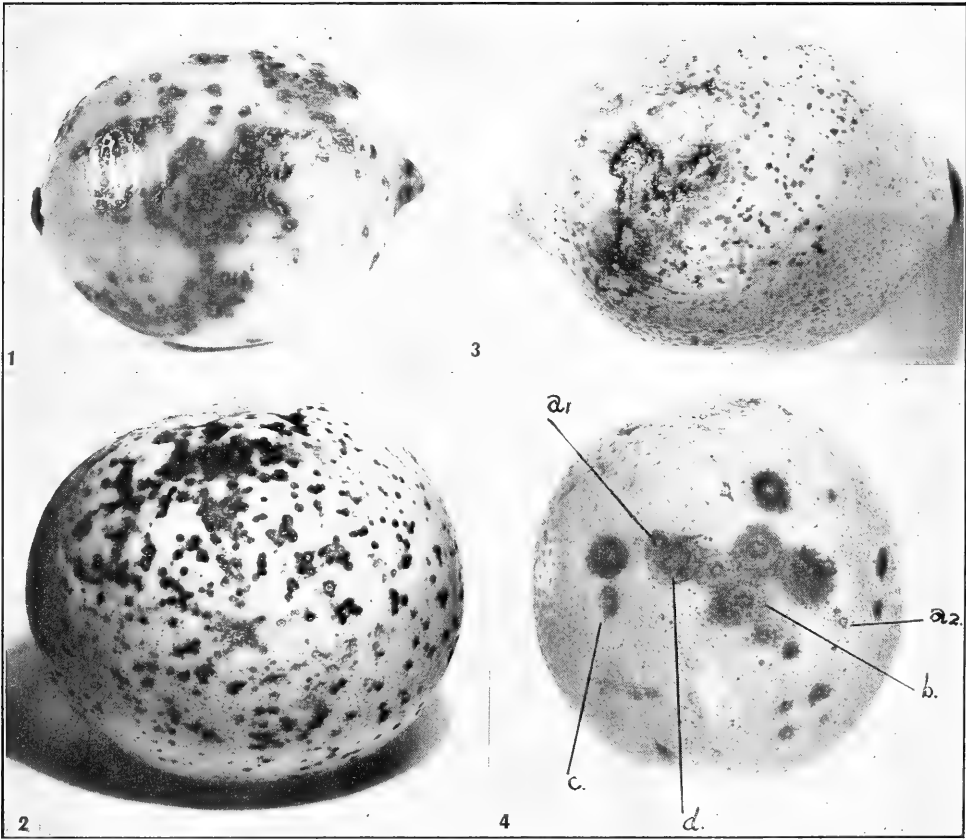
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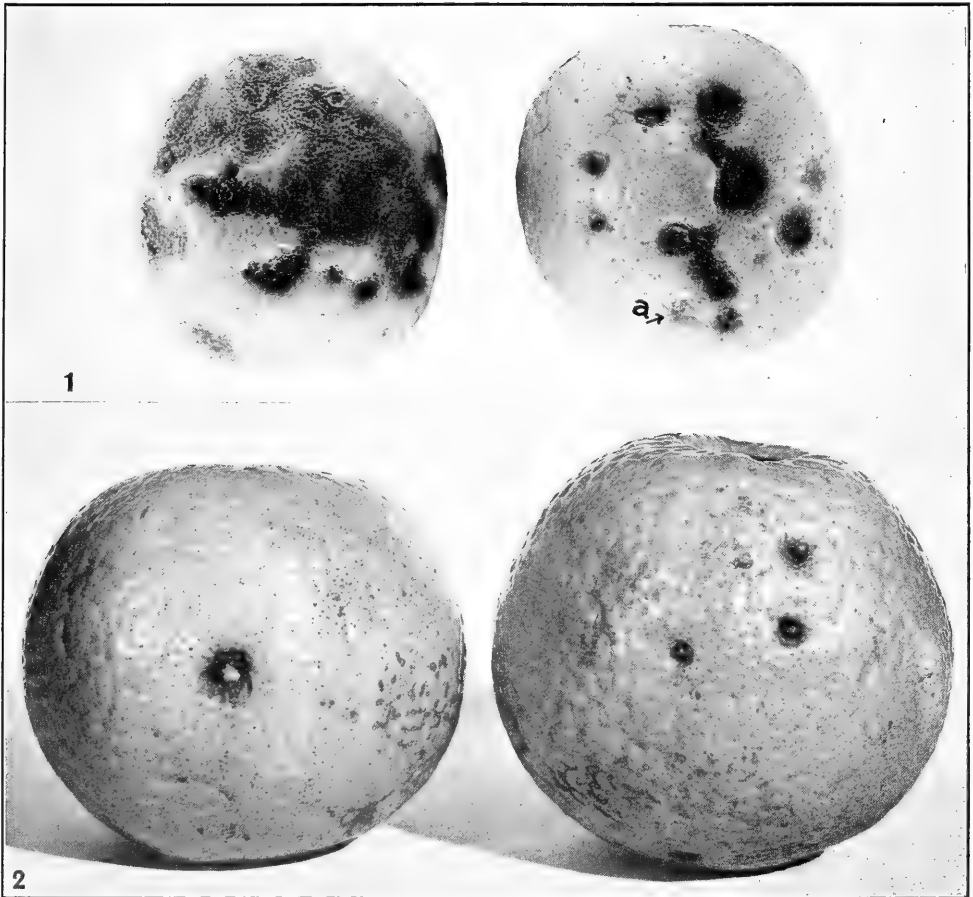
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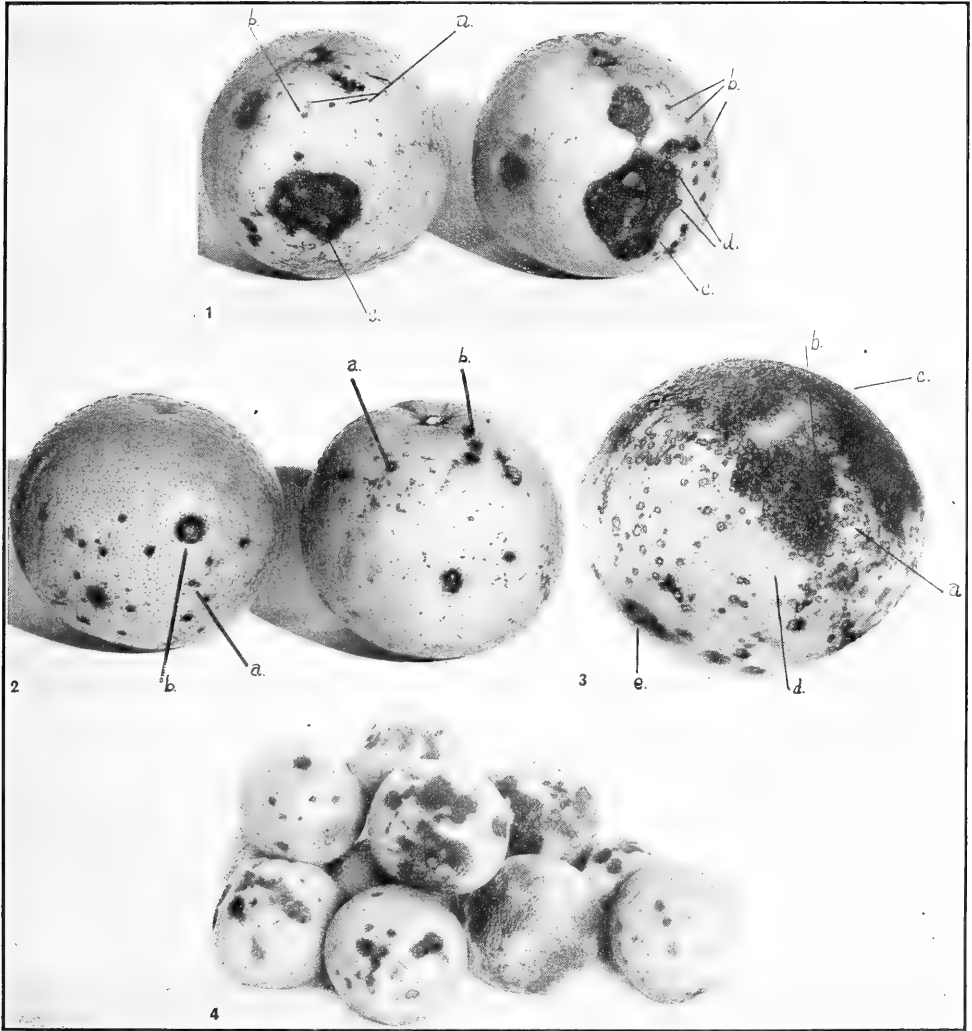
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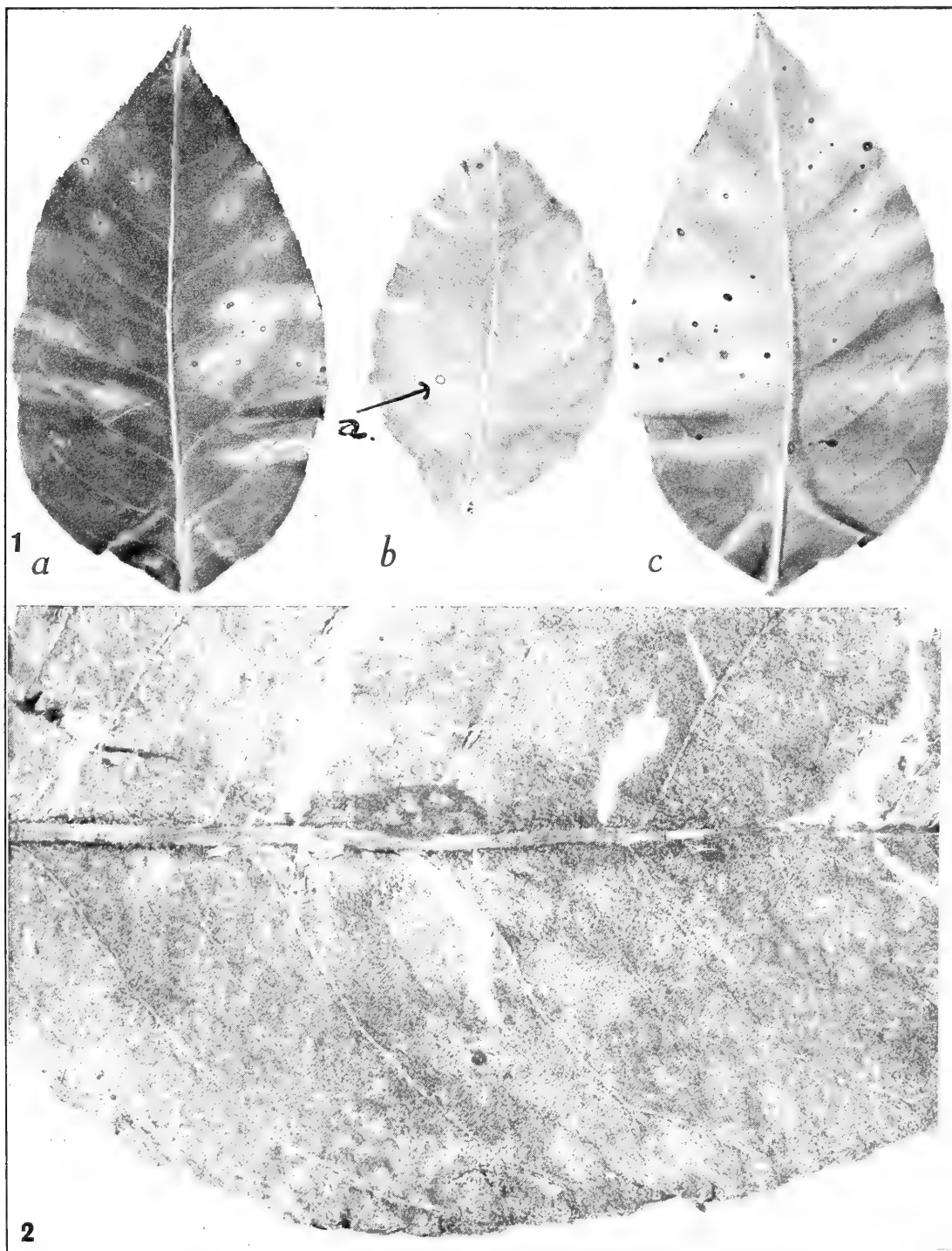
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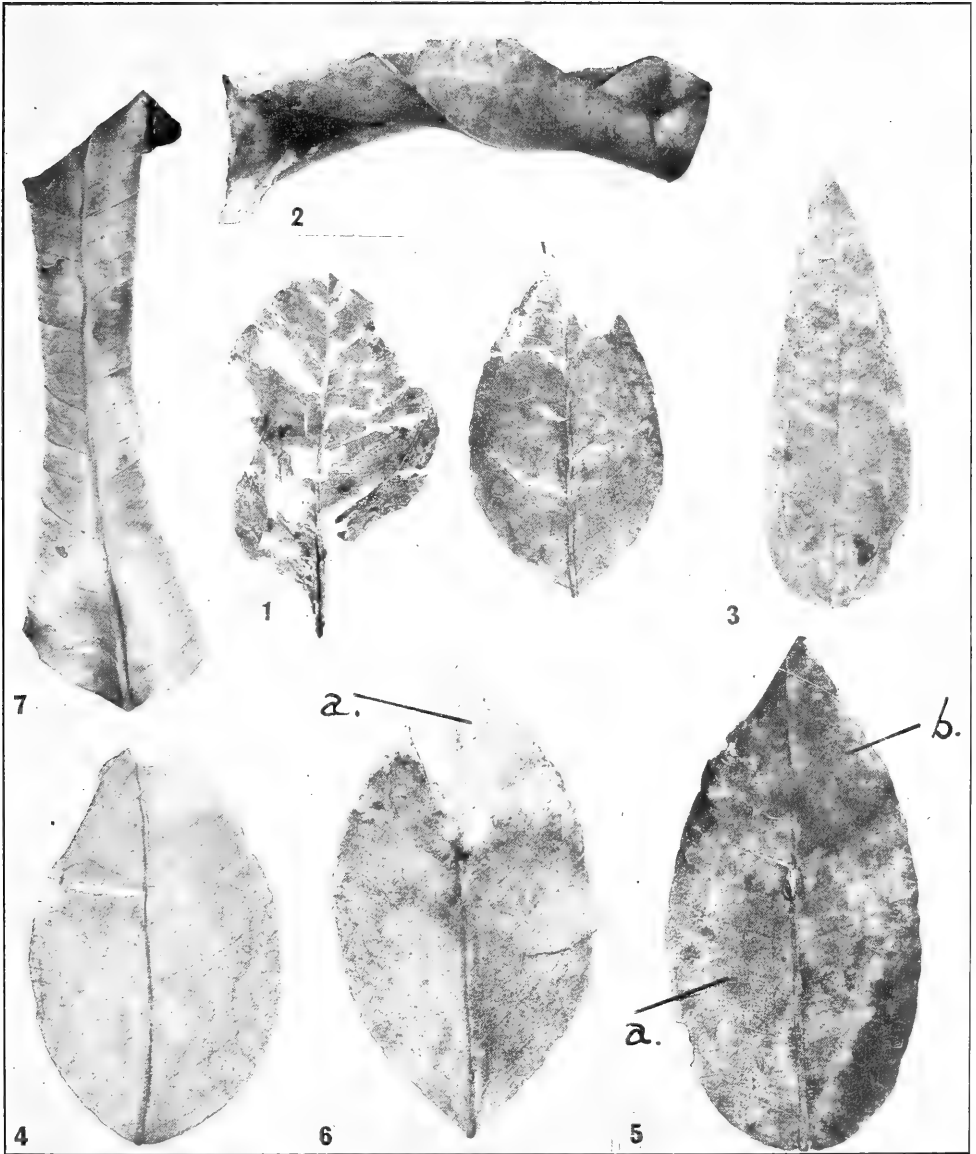
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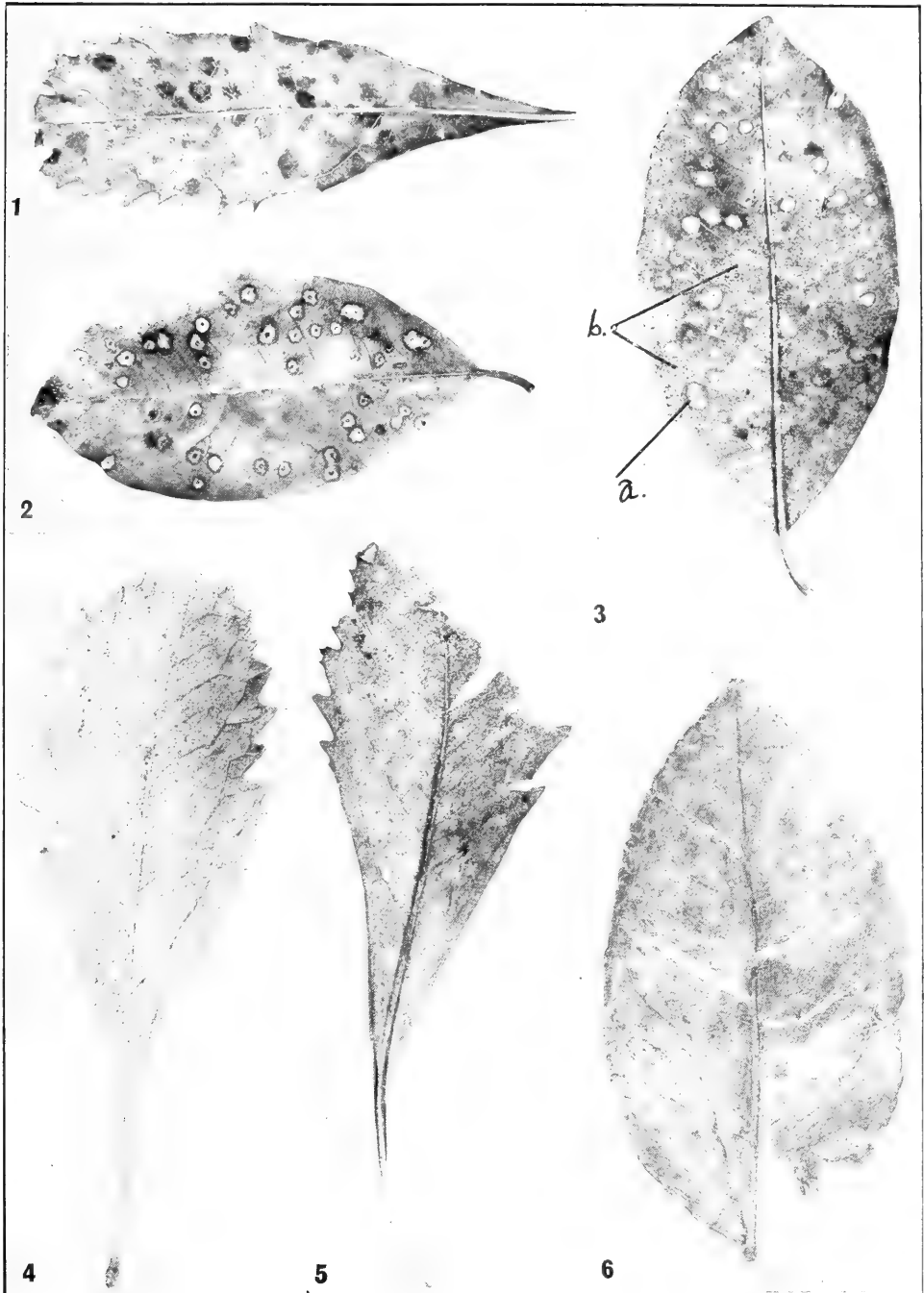
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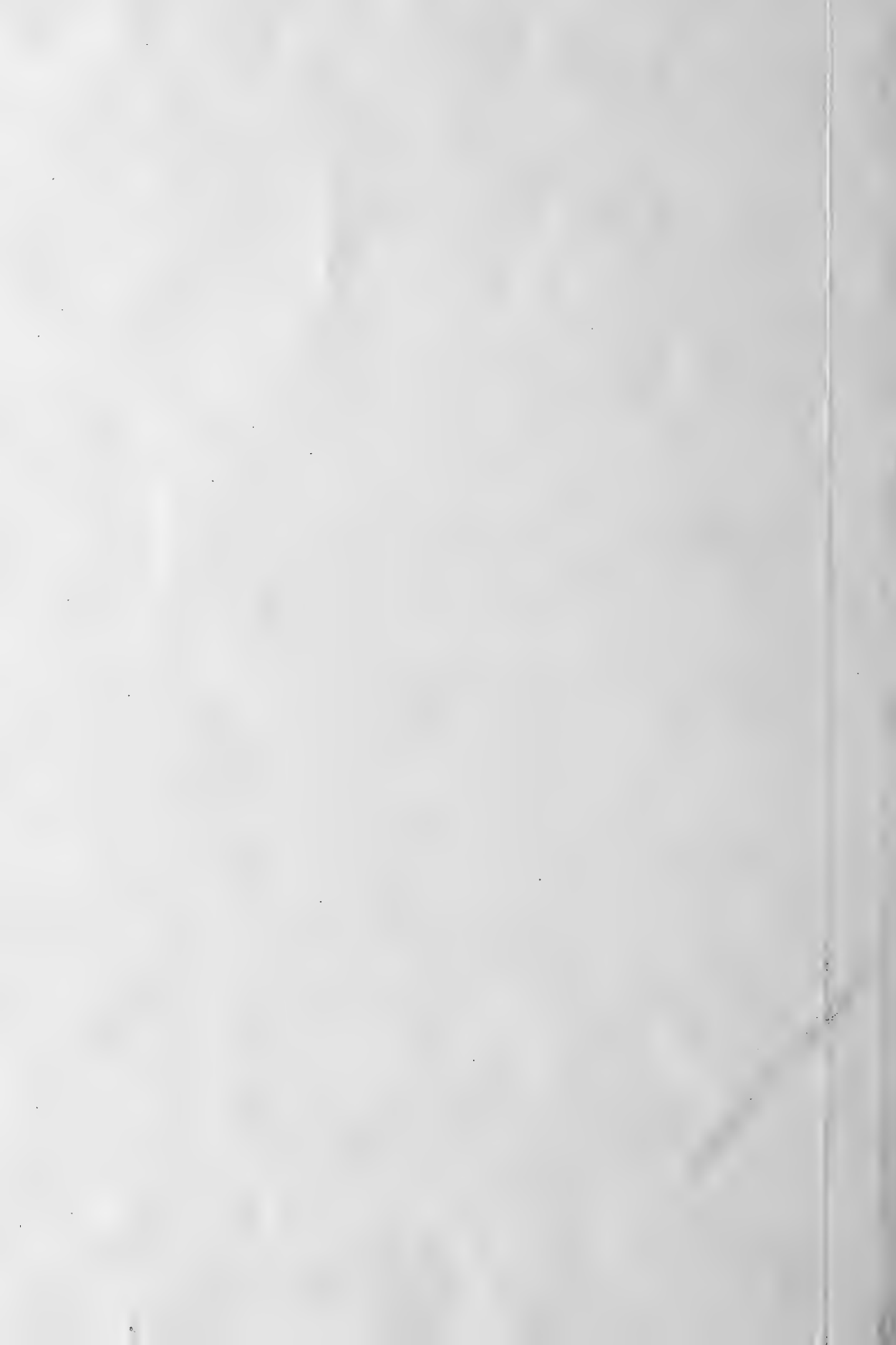
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1929 ..	LIV	2 0	6 3	8 6	11 0	12 6	2 0
1930 ..	LV	2 0	10 0	8 9	8 6	16 3	2 0
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1932 ..	LVII	6 6	9 6	8 6	1946 ..	LXXI	6 9	13 0	9 0
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1928 ..	LIII	2 0	8 6	8 9	10 0	9 0	2 0
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