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ANNUAL GENERAL MEETING.

WEDNESDAY, 27th MARCH, 1940.

The Sixty-fifth Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 27th March, 1940.

Professor J. Macdonald Holmes, B.Sc., Ph.D., President, in the Chair.

The minutes of the preceding Annual General Meeting (29th March, 1939) were read and confirmed.

PRESIDENTIAL ADDRESS.

The year 1939 was a year of great promise for this Society. Though much has been accomplished, it will be looked back upon as a great turning point in the scientific work of our members. The researches of Peace are being put aside for a time—we are becoming engrossed, nay, embroiled, in the labours of War. It is pertinent, therefore, that I should review briefly for you the year's work, and that my address should have the form of a stock-taking.

The concluding part of Volume lxiv of the Society's Proceedings was issued in December. The complete volume (608 plus lxvii pages, twelve plates, and 499 text-figures) contains forty papers on various branches of Natural History. The volume is larger than usual; this is due to some financial assistance received towards the printing of a series of papers on the Diptera of the Territory of New Guinea.

Exchanges from scientific societies and institutions totalled 1838 for the session, compared with 1795, 1865 and 1860 for the three preceding years. The following additions have been made to the list of societies with which an exchange of publications is maintained: Department of Zoology, University of Sao Paulo; Entomological Society of Southern Africa, Pretoria; Instituto Botanico de la Universidad Central, Quito, Ecuador; and Instituto de Botanica Darwinion, Buenos Aires.

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

JOSEPH WILFRID DWYER, D.D., Bishop of Wagga, who died at Wagga on 11th October, 1939, was born at East Maitland on 12th October, 1869. He took a keen interest in the study of the Australian flora and had been a member of this Society since 1920.

WILLIAM BUTLER GURNEY, who died in Sydney on 21st September, 1939, was born at Sydney on 2nd May, 1882. He entered the service of the N.S.W. Department of Agriculture in 1900 as assistant to the late W. W. Froggatt, whom he succeeded as Chief Entomologist in 1923. He graduated Bachelor of Science at the University of Sydney in 1925. As delegate from New South Wales he attended the 4th International Congress of Entomology at Cornell University in 1928, and subsequently toured the United States of America, and visited England, France and Italy in 1928–29. He also later visited India and East Africa to study insect pest control methods. The results of his entomological investigations were

published chiefly in the Agricultural Gazette of New South Wales. He had been a member of this Society since 1901, and was also a Fellow of the Royal Entomological Society.

André Leon Tonnoir was born in Brussels on 9th April, 1885. After his formal education at school and Liége University, he spent several years travelling in England, France, Germany, Italy and Spain. During this period he was able to give much of his time to his outstanding interest, entomology, and, incidentally, to acquire a sound knowledge of six languages. However, it was not until after the Great War, when he was appointed to the staff of the Brussels Natural History Museum, that he was able to devote his whole time to his former hobby. Like many naturalists, he was especially interested in Australia and New Zealand, and in 1921 he accepted a commission to study the dipterous insects of the temperate zone of the Southern Hemisphere, a study which still occupied his leisure hours up to the day of his death. He went to New Zealand, where he worked at the Cawthron Institute, the Canterbury Museum, and the Canterbury University College until 1929, when he joined the staff of the Council for Scientific and Industrial Research in Canberra. During the past ten years he had been closely associated with research on biological control of insect pests and weeds, and he also played a prominent part in the development of an intensive study of the grasshoppers in Australia. His numerous papers on lesser-known families of the Diptera do not adequately reflect his remarkably wide knowledge of insects, although they are a record of the thoroughness of his work and his outstanding ability as a taxonomist. He died on 27th January, 1940, at Uriarra, thirty miles from Canberra, peacefully in his sleep as he rested in the shade of a tree, after a morning's collecting.

Frederick Wright died at Lane Cove on 17th December, 1939, at the age of eighty years. He had been on the staff of Elliott Brothers, later Elliotts and Australian Drug Pty., Ltd., for sixty-six years. He had charge of the Pharmacy course at the Sydney Technical College from 1881 until its transference to the University of Sydney, after which he lectured in various subjects of the course. He had been a member of the Society since 1925.

Reference may here be made to the death of Fred Turner at Chatswood in October, 1939, at the age of eighty-seven years. Mr. Turner was a member of this Society from 1891 to 1923 and a member of Council from 1897 to 1912. He was widely known for his works on botany and horticulture.

In December Mr. A. G. Hamilton tendered his resignation as a Councillor. Mr. Hamilton had been a member of Council since 1906, and his resignation was accepted with great regret, it being resolved that there be placed on record in the minutes an expression of appreciation of his services to the Society over a very long period. In view of these services your Council unanimously elected Mr. Hamilton, a Corresponding Member of the Society.

In December last the Premier of New South Wales announced that new appointments of Trustees of the Sir Joseph Banks Memorial Fund would be made by a bill to be introduced into Parliament in 1940. It was stated that the trustees would include the President of the Legislative Council, the Speaker of the Legislative Assembly, the Public Librarian, and one representative of each of the following societies: The Naturalists' Society, the Royal Zoological Society, the Royal Australian Historical Society and the Linnean Society. It is gratifying to learn that at last there is some prospect of the fund being used to commemorate the life and work of Sir Joseph Banks.

During the year, representations were made, in support of those by other scientific bodies, to have restrictions placed on the export from Australia of geological specimens, similar to those already in force regarding zoological specimens. It is understood that the Commonwealth Government has decided to take the necessary action to impose such restrictions.

We offer congratulations to four members who attained their doctorates during the year: Drs. H. G. Raggatt, C. J. Magee, H. L. Jensen and S. W. Carey; also to Professor W. N. Benson, who, during 1939, was awarded the Lyell Medal by the Geological Society of London—previous Australian recipients being Mr. F. Chapman (1930), Mr. E. C. Andrews (1931) and the late Professor W. Howchin (1934).

During the winter of 1939 the far west division of New South Wales received an unusually large rainfall, and it was suggested that advantage be taken of the opportunity to study the flora in this unusually good season. Several small parties visited the district, and this Society made a small grant in support of the expenses of these expeditions. Valuable records were obtained, and a series of photographic records, taken by one party, has been presented to this Society.

Early in 1939 the Macleay Bacteriologist proposed to embark on a programme of research concerned with the nitrogen-fixing bacteria of our soils. To carry out this programme it was necessary that a plant house should be available, and it was desirable that some assistance should be provided for the large amount of routine work involved. The Bacteriology Committee of the Council therefore approached several of the banking institutions with a request for financial assistance to enable this programme to be carried out, in view of the fact that it concerned soil fertility, a subject of prime importance to Australia and to those institutions in particular which have financial relations with the primary producers. I am pleased to be in a position to state that the authorities of the institutions concerned (Commonwealth Bank of Australia, Rural Bank of New South Wales, Bank of New South Wales and Commercial Banking Company of Sydney, Ltd.) received the request with every sympathy and have provided sufficient funds for the erection of a plant house and for the employment of an assistant to the Bacteriologist for a period of three years. The construction of the plant house is almost complete, and from nineteen applicants for the position of Biochemist the Council selected Mr. R. J. Swaby, B.Agr.Sc., of the University of Melbourne. Mr. Swaby took up his duties on 1st December, 1939. The thanks of the Society have been tendered to the Banks for this generous assistance to the cause of Science.

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

Dr. H. L. Jensen, Macleay Bacteriologist to the Society, has carried out, as a sequel to the experiments on nitrogen fixation in wheat soils, a series of experiments on symbiosis between cellulose-decomposing and nitrogen-fixing bacteria. It has been found that the common aerobic cellulose-decomposers (*Cytophaga*, *Cellvibrio* and related bacteria, besides fungi and actinomycetes), which are usually considered the most important under soil conditions, are unable to provide nitrogen-fixing bacteria with available food material from cellulose. Certain other bacteria, probably hitherto unknown, are able to do so; combined cultures of these bacteria and *Azotobacter* can fix from 6 to 14 mgm. N per gm. of cellulose decomposed. This may be claimed to be the first instance where such results have been obtained with pure cultures. These high gains are only found in solution cultures, and not where the access of oxygen is complete, such as in

well-aerated soil. This explains readily why high moisture content of the soil is necessary for nitrogen fixation on the basis of cellulosic materials. Further work on the physiology of these organisms, especially their formation of soluble organic compounds from cellulosic materials, is in progress. A number of strains of root-nodule bacteria from wild legumes have been isolated for future work. As a supplement to the last few years' work, numerous wheat soils have again been tested for the occurrence of *Azotobacter*. No evidence has been found that this organism becomes active after periods of heat and drought or that it is particularly common in association with the roots of leguminous plants. A search has also been made for special acid-resistant types of *Azotobacter*, described recently by Indian and American investigators; such organisms do not seem to occur in Australian soils.

The Royal Veterinary and Agricultural College of Copenhagen has approved, for the degree of Doctor Agronomiae, the thesis entitled "Contributions to the Nitrogen Economy of Australian Wheat Soils, with particular Reference to New South Wales", submitted by Mr. Jensen. This thesis is to be published in the next Part of our Proceedings.

Miss Elizabeth Pope, Linnean Macleay Fellow of the Society in Zoology, continued the preparation of the results of her ecological work at Long Reef for publication. The first part of this work is an introduction to the animal ecology of the reef and deals with the environmental factors. In a second part it is intended to describe and list the animals in the various communities and, if possible, to indicate their inter-relationships. Miss Pope also completed an extensive revision of the muscular system of the Port Jackson Shark. On 14th September, 1939, Miss Pope resigned in order to accept an appointment on the staff of the Australian Museum.

Miss Ilma Pidgeon, Linnean Macleay Fellow of the Society in Botany, continued her studies of the vegetation of the district round Sydney and has completed Part iii of the series of papers on the "Ecology of the Central Coastal Area of New South Wales", which deals with types of primary succession. In August she visited Broken Hill and conducted investigations into the colonization of the fenced and unfenced areas south and west of the town. Statistical methods were used in these studies and the results are incorporated in a paper, written in collaboration with Professor Ashby, entitled "A Statistical Analysis of Regeneration following Protection from Grazing", which is to appear in the next Part of the Proceedings. Miss Pidgeon has also commenced work on the comparative anatomy and physiology of the juvenile and adult forms of *Eucalyptus globulus*, and has undertaken an investigation of the differential effect of various washing solutions on the loss in weight of oranges.

Miss Valerie May, Linnean Macleay Fellow of the Society in Botany, has completed an experiment on drought resistance of two varieties of Oats (Algerian and Fulghum). The new technique of measuring increment of height to obtain differences in response to and recovery from drought has proved satisfactory. Varietal differences in response to drought have been proved statistically. The effect of manuring on resistance to drought is being followed further in an experiment on sun-flowers at present in progress and yielding encouraging results. Two papers, "A Key to the Marine Algae of New South Wales. Part 2. Melanophyceae (Phaeophyceae)" and "*Ectocarpus confervoides* (Roth) Le Jol", were published in the Proceedings for 1939.

Miss Margaret Cumpston, Linnean Macleay Fellow of the Society in Zoology, began her experiments with an investigation on the strawberry pest *Sericesthis pruinosa* which was bred through to the adult rapidly at controlled temperatures, but it was found that the conditions were unsuitable for mating and oviposition since no eggs were obtained from the adults. With the material from these experiments investigations were carried out on the changes in weight and water content during metamorphosis. Further observations were instituted with the species under field conditions. Studies of the biology and morphology of *Heteronychus sanctae-helenae* and *Metanastes vulgivagus* have been carried out and the results are almost ready for publication. One paper, "Observations on the Bionomics and Morphology of Seven Species of the Tribe Paropsini", was published in the Proceedings for 1939.

Five applications for Linnean Macleay Fellowships were received in response to the Council's invitation of 27th September, 1939. I have pleasure in reminding you that the Council reappointed Miss Ilma M. Pidgeon, Miss Margaret Cumpston and Miss Valerie May to Fellowships in Botany, Zoology and Botany respectively for one year from 1st March, 1940, and appointed Mr. J. A. Dulhunty, B.Sc., to a Linnean Macleay Fellowship in Geology for one year from 1st March, 1940.

Mr. John Allan Dulhunty graduated in Science at the University of Sydney in 1938 with First Class Honours in Geology, and was awarded the Deas Thomson Scholarship in Geology for 1938. During the years 1938 and 1939 he was Demonstrator in Geology at the University of Sydney. He has carried out a series of stratigraphical and structural studies in the Talbragar, Merriwa–Murrurundi, and Gulgong–Coolah districts and has also done some preliminary laboratory work on the essential constituents of the Torbanites of New South Wales. The results of his work have been included in a series of five papers published in the *Journal of the Royal Society of New South Wales*, Volumes lxxi–lxxiii.

During the coming year Miss Pidgeon proposes further work on the comparative anatomy and physiology of *Eucalyptus globulus*, and also additional statistical studies of the regenerating vegetation at Broken Hill; she also proposes to continue work on the effect of various detergents on the loss in weight of oranges. Miss May aims to expand the work on drought resistance, in the hope that the results may prove finally to be of some economic significance in the more arid regions. Miss Cumpston has unfortunately found it necessary to resign her Fellowship. Before this takes effect she hopes to complete the work on *Heteronychus sanctae-helenae* and *Metanastes vulgivagus*, and to prepare a bibliography of the literature of this group of Coleoptera, in order that the work she has done shall be readily available for any future worker on the group.

Mr. Dulhunty proposes to study the constitution, origin and developmental history of the torbanite (oil shale) deposits of New South Wales. We wish them all a successful year's work.

The Science of the Soil.

A STOCKTAKING OF PRESENT TRENDS.

This century has seen a great renaissance in soil studies. By far the greatest interest is in problems which find themselves on the border lines of what used to be called the "main branches of science", and therefore much of the recent literature on soil is found under climatology, botany, geology, chemistry, as well as under agriculture and forestry. More recently, geographical distribution methods have been applied to soil surveys with considerable success, and, under the impetus of modern roadmaking, engineering has been incorporated in the above group.

But, struggling along in the wake of this renaissance, are a whole group of problems which can be classed under soil sociology. Indeed, this latter aspect bids fair to eclipse all other soil studies from the point of view of expenditure and human needs. In the United States of America, for example, the human and economic problems connected with soil wastage, especially in the wheat, cotton and tobacco belts, have forced the Soil Conservation Services to make intensive soil studies which practically amount to a reorganization of Soil Science.

Contemporaneous with this great renaissance in ideas connected with the soil, there has become established the truism that "in the soil we have a natural object capable of independent study and subject to the scientific rules of nomenclature and of classification" . . . and that "it is no longer necessary to seek a geological, a climatic or an ecological basis for soil classification".[1] Indeed, Marbut sums up the situation thus: "To define and classify soils under these circumstances on the basis of their relation to geology, climate, natural vegetation, or crops can be justified only as a temporary expedient. This stage in soil investigation has been passed. It has become possible, and therefore obligatory, in a scientific sense at least, to define and classify soils on the basis of the soils themselves."[2] In this manner has the new Soil Science defined itself.

So, in spite of this widespread soil renaissance, emanating from many branches of science, the new Soil Science is determined to seek the narrow path. Soil Science will then be limited to a study of those few inches of the "uppermost layer of the earth's crust which is subject to the influence of atmospheric and biological forces",[3] and, with its present technique, to that part of the soil's surface which is capable of passing through a two-millimetre sieve. Soon, it could be argued, only such study as the microscopic and X-ray examinations of colloidal clay soil content will constitute Soil Science, and the few prominent scientific workers thus attracted are not likely to indulge in those field studies on which our hopes are based.

The Implication of the new Soil Classification.

Now Prescott's classification, restricting Soil Science to the zone of atmospheric and biological agencies, is at once too narrow and too wide—too narrow if the science is restricted to a not always easily recognizable topmost zone of recent weathering, and too wide since atmospheric and biological agencies are often very effective deep down in the solid rock, as the many instances of deep weathering testify.

[1] Prescott, "The Classification and Mapping of Soils", *A.N.Z.A.A.S.*, Vol. 23, Auckland, 1937, p. 271.

[2] Atlas of American Agriculture, 1936, "Soils of the United States", p. 11.

[3] Prescott, "The Classification and Mapping of Soils", *A.N.Z.A.A.S.*, Vol. 23, Auckland, 1937, p. 258.

In actual practice, Soil Science is restricting itself to only certain work within this wide zone of weathering; for example, the work of Dr. Jensen, Macleay Bacteriologist to the Society. Perhaps the most fundamental aspect of the new science is the importance attached to the examination of soil profile (i.e. changes with depth), and the significance of soil colour types. Now, soil profiles differ very frequently, so there is an effort to group them into generalized forms which will be distinctive over a wide area. Profile changes are chiefly chemical and textural, and such changes supposedly result from present-day climate and vegetation, so that while each soil receives a type-name based on texture and a geographic name based on locality, the final classification of major soil groups is fundamentally environmental. The omission of an environmental term earlier in the classification is unfortunate.

But even this environmental grouping has not been fully followed out, as the list of World Soil Groups clearly shows. "The groups are Tundra soils, Podzols, Gray-Brown Podzolic soils, Red soils, Yellow soils, Prairie soils, Laterites, and ferruginous Laterites, Chernozems, Dark-Brown soils, Brown soils, Gray soils."[4]

The chief practical consideration in the new Soil Science, therefore, is that in its search for consanguinity between soil types and soil groups there still is an appeal to forces which are continually making and remaking the soil: and indeed perhaps to the historical forces which by several cycles of events created the superficial deposits of the Earth.

On the contrary, there is the challenging implication that the new Soil Science is sufficient unto itself, which is the more to be wondered at in that its exponents regard soil as a product. For example, Marbut states: "Soils are the product of environmental conditions under which they have developed or are developing."[5] But earth history is such that it would be preferable to think of soils as a by-product of certain deposits, which themselves are the product of the interactions of atmospheric agencies, past and present, upon the earth's structural surface. These forces, being constantly at work, make soil an ever-changing by-product.

The climatic challenge to the geological interpretation of soils was fought on too simple premises which obscured the real issue. It is readily conceded that the same soil (in the restricted sense) may cover many types of rock formation, and may even, though less frequently, cover different types of soil-forming deposits, but can there be a complete soil description which fails to account for the superficial deposit (drift) to which the soil owes its continued existence, and takes little note of the topographic site and climatic situation which moulds its character?

The real issue is that soil study had to be freed from the outworn techniques in geology and agriculture before it could be rightly of service to geology and agriculture.

Again, soil mapping, or what has come to be called Soil Survey, if it is to be successful, must abide by the essence of mapping technique, namely, to work from broad generalizations towards detailed sampling, where again site and situation lend themselves to successful application. The recognition of A and B horizons in a profile acknowledges the changing nature of soils, a factor which is closely related to the climatic situation of the soil and its topographic site, and for which a term must be found in any final classification.

[4] Atlas of American Agriculture, 1936, "Soils of the United States", p. 13.
[5] Ibid., p. 1.

Great care should be exercised that soil mapping is not too far ahead of the study of the things being mapped. Too great zeal for mapping technique *per se* has had the result in New South Wales of leaving topographic mapping far behind in general scientific progress.

The new soil science makes this further challenge, that there is such a law as the law of soil genesis as stated by W. W. Weir (*Soil Science*, 1936, p. 138), according to which "the same natural forces acting under like conditions upon deposits of loose geologic material produce identical characteristics".

Finally, does not the new conception of soil involve several questionable assumptions?—e.g.

(1) that the chief soil-forming forces are external, i.e. that if the precipitation, vegetation and temperature are known, then the soil types are known,

(2) that these forces have operated separately and collectively as at present and sufficiently long to discount the nature of the soil deposit material and its potentialities for mass change.

Any dynamic philosophy of earth study can only admit these assumptions to be true as tendencies, and they can only be sufficiently true for a field soil science where the climate is temperate, the vegetation prolific, the topography gentle, and where drainage is effective but slow, and where the fire stick and the plough have not disturbed the land, i.e. where the total soil content is colloidal.

The exceptions are too many for such a scheme as set out below (see Fig. 1) to prove adequate for long.

Categories	Factors that determine soil characteristics on which principal classes are based	Soil classes	
		Soil	
V	Soil leaching	Pedalfer x. *Podzolic soils* y. *Lateritic soils*	Pedocal x. *"Carbonatic" soils* y. *"Alkalitic" soils*
IV A	Climate	Gray forest Brown forest Red and yellow Tundra (dry) Lateritic and Laterite	Chernozem "Chestnut-brown" Brown grassland Desert
IV B	Prairie grasses	X. Prairie soils	X. Prairie soils
IV C	Ground water and water of permanent saturation	X. Hydromorphic soils x. *Organic* y. *Inorganic*	X. Hydromorphic soils x. *Organic* y. *Inorganic*
III	Sameness of parent material	Family groups	Family groups
II	All soil-forming factors except texture	Soil series	Soil series
I	All soil-forming factors	Type groups	Type groups

Fig. 1.—A comprehensive scheme of soil classification, showing natural order in soils as determined by the law of soil genesis. (After W. W. Weir.)

While we are ready to agree that this soil science, which "has already a literature and philosophy of its own", should be "separate and independent", is it not, in the nature of things, divorcing itself from a wider field which is the real science of the soil?

We propose now to examine this wider field of soil and soil deposits, and have selected several outstanding aspects and grouped them for convenience into the branches of science to which they seem cognate.

Chemical Problems cognate to Soil Science and Soil-deposit Morphology.

The most fundamental and far-reaching work in the new Soil Science in Australia is the work of the Division of Soils, under Professor Prescott, at the Waite Institute in Adelaide. Since the excellent discussion of the general distribution of the chief soil groups in Australia, in Council for Scientific and Industrial Research Bulletin 52, 1931, there has been a succession of Bulletins, each being a detailed survey of a small district, and each Bulletin supported by a large-scale soil map. Essentially, each of these surveys gives a detailed description of the various soil profiles as examined in the field. Accompanying these descriptions is a chemical and mechanical analysis, and in some Bulletins a discussion of "Base Exchanges". There are elaborate tables giving the chemical and mechanical analysis of soil types, which should prove invaluable to field agriculturists. A later Bulletin (Bulletin 118) makes an advance on the earlier ones by grouping the soils "according to topography and mode of development", as well as to their relations with the world zonal groups. Over an area of 19,800 acres, it has been possible to make the following five groups:

"(i) Soils of the plain—alluvial origin.
(ii) Soils of the hill slopes—colluvial origin.
(iii) Windblown sandy soils—aeolian origin.
(iv) Soils of mixed origin.
(v) Mallee soils."

Apart from this concession to geomorphology, the remainder of the Bulletin is a characteristic chemical and physical description, invaluable in itself and to agriculture, but from which it is difficult to obtain that information which one requires for an understanding of the place of soil in any scheme of Earth Study.

As Prescott has indicated, the soil work of the Council for Scientific and Industrial Research in Australia has been left principally in the hands of soil chemists and agriculturists, even in the mapping work. New Zealand, on the other hand, has left the mapping to geologists, and the laboratory work to agricultural chemists, which gives to their published work a character different from that of Australia. Nevertheless, the treatment given to soil in these two countries is indicative of the breadth that exists in this new soil science. But in New Zealand (and she is not alone in this) it would appear that the new terminology in the laboratory is an embarrassment to the field studies.[6]

In the United States, the Division of Soil Surveys comes under the Bureau of Chemistry and Soils, in the Department of Agriculture. Most elaborate studies of all kinds have been made, but the soil work has been most diligently summed up in the American Atlas of Agriculture, Part iii, 1935. Again, this is an elaborate mechanical and chemical description and classification of soils into world groups and geographical type names. Yet withal, this valuable and voluminous atlas and text-book of soil cannot be said to make a great contribution to land study, great as is its contribution to the narrower field of Soil Science. It may be that the weakness rests with the other branches of science because of their inability to make use of the new knowledge.

[6] Report on Soil Surveys, 1935/36, Department of Scientific and Industrial Research, Wellington.

In contrast to this descriptive soil chemistry, on which all the above studies are based, and which should be well known to you, there is the soil work of Polynov, described in his book "Cycle of Weathering". This treatise shows that the chemical changes which take place in the common elements of the earth's crust occur in cycles, and that the form in which the element is found in the crusty deposits of the earth's surface is indicative of its weathering history. There are, for example, (i) the oxygen, carbon and nitrogen cycles, (ii) the silicon, aluminium and iron cycles. There is much in common between this physiographic study of Polynov and the newer soil science; for example, in regard to lime and carbonates he has found that in practically every soil type in arid and in semi-arid regions there are lime horizons, and a considerable variety of lime-bearing minerals; and that carbonates are typical products of sub-aerial weathering.

In the new Soil Science the presence or absence of lime horizons places soil types in one or other of the great soil groups, namely, pedocals or pedalfers.

But Polynov goes further, and shows that the chemical and mineralogical characters of weathered deposits have a topographical distribution in relation to the stages in the weathering cycle. Briefly, Polynov's classification of types shows the following forms, which he claims are genetically related, and "this relationship is shown ultimately in the dependence of their distribution on geomorphic conditions".[7]

"I. Residual: (*a*) coarse detrital, (*b*) calcareous, (*c*) siallitic,[8] (*d*) allitic orthoeluvium.

II. Accumulative: (*a*) chloride-sulphate (predominantly alluvial), (*b*) calcareous (predominantly colluvial and proluvial), and (*c*) siallitic drifts."

The geomorphological conditions he sets out as follows:

"I. The calcareous orthoeluvium of watersheds is accompanied on the lower levels by an accumulative chloride-sulphate crust of weathering in the form of a drift (enriched with chlorides and sulphates). The salt catchment region for chlorides and sulphates is the whole thickness of the residual crust of weathering on the watershed, (Gobi type).

II. The siallitic orthoeluvium of watersheds is accompanied on the lower terraces by calcareous accumulative, and still lower, by chloride-sulphate crusts of weathering. In this case the whole thickness of orthoeluvium serves as the source of carbonates for the calcareous accumulation, whilst the chloride-sulphate crust receives its material from the orthoeluvium, and the calcareous accumulation, (Northern Mongolian type).

III. Allitic orthoeluvium of watersheds is accompanied by the distribution over lower levels of the following in the order given: siallitic, calcareous, and, at the lowest level, the chloride-sulphate crusts of weathering, (Congo and Zambesi basin type)."

His theoretical diagram is worthy of introduction (see Fig. 2).

But, as Polynov is aware, superimposed upon this primary cycle there are several others, the overlapping of which makes soil types a more complex distribution. Nevertheless, the elucidation of the stages in this primary cycle is applicable to much of Australia, because there are enormous areas of primary crystalline and ancient metamorphic rocks.

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[7] B. B. Polynov (trans. Muir), "Cycle of Weathering", 1937, p. 176.

[8] Siallitic means colloidal synthesis of silica and alumina. Allitic means alumina gels and their derivatives. Orthoeluvium means coarse detritus of primary (igneous) rocks.

Again, Polynov makes an interesting contribution in regard to the influence of climate on weathered deposits. On the assumption that one-third of the precipitation is lost by evaporation, and that the total silica in the rock amounts to 40%, it would take fifty thousand years for the complete allitization of a one-metre layer of rock. But this estimation was made from rock powdered for laboratory experimentation, wherefore conditions in nature must be very much slower.

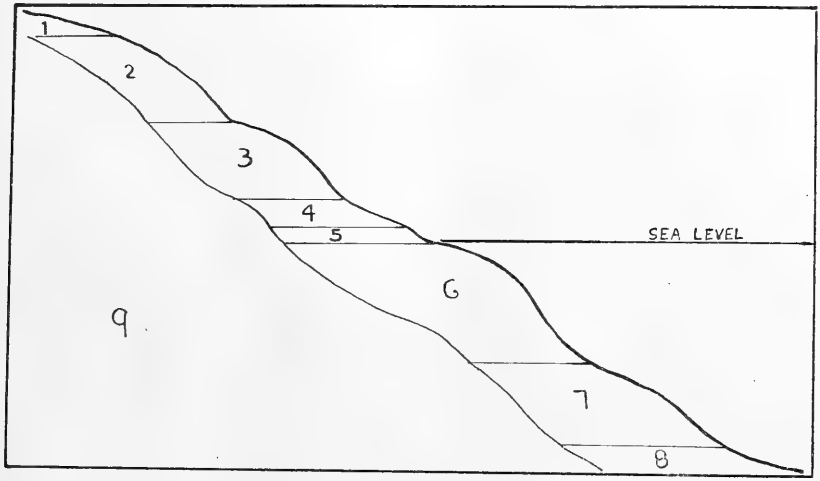

Fig. 2.—1, Allitic eluvium; 2, Siallitic (allophanic) accumulation; 3, Carbonate accumulations; 4, Chloride-sulphate accumulations; 5, Coastal deposits; 6, Terrigenic muds; 7, Pelagic muds; 8, Deep-water red clay; 9, Massif of igneous rock.

The perplexing problem in Australia is that there are extensive areas of gentle slopes which have been exposed to atmospheric agencies since Permian and Triassic times, and yet only possess an inch or two of soil.

Polynov observes that "it is well-known that real examples of the formation of allitic products of weathering are confined to regions with a moist tropical climate which, *at the same time*, are the regions of the most ancient land (India, Amazonia, etc., referred by Suess to the ancient Gondwanaland)".[9] He quotes Harrassowitz as being unable to find "any clear indication of a lateritic crust of weathering on sedimentary, and observed it only on the more ancient igneous and strongly metamorphosed rocks", and he comes to the conclusion that "the formation of an allitized crust of weathering is confined to the regions of moist tropical climate, not because this process is exclusive to that climate, but because at the present geological epoch the process of allitization has reached its greatest development in countries of the most intensive weathering, i.e., of moist tropical climate".[10]

Later he "arrives at the general conclusion that climate, that is, the hydrothermal conditions of weathering, has a substantial influence on the intensity of that process *without altering in the least its general direction*; and if at the present time we find that the calcareous orthoeluvium and accumulations are

[9] Ibid., p. 178.
[10] Ibid., p. 179.

confined to dry steppe climate, and allitic orthoeluvium to a moist tropical climate, this is so, not because each climate has its own independent type of weathering, but because the processes of weathering at the present moment have attained different stages, viz., those that we now observe. This circumstance explains why the climatic factor appears to dislocate our scheme for the distribution of the products of weathering which was built up solely on a geomorphological basis".[11]

Now much of the surface of Australia and many of the inland soils are lateritic, and Woolnough takes the view that lateritic and corresponding siliceous materials were formed as a duricrust deposit. But duricrust now has the appearance of a well-defined bedded rock which is the topmost zone of the extensive flat-topped plateaux of inland Australia. He accounts for the formation of duricrust as a sweating-out product from an extensive previous deposition of highly siliceous material. But it is important not to confuse the widespread pebbly laterite, and the gibbers, with duricrust, since this loose stony deposit is a reassemblage composed not only of weathered laterite and duricrust but also of pebbles from rock much older than duricrust, and also from a reweathering of even older rocks. Of this I will say more later, but the lateritic question is important to Soil Science, and also to pastoral and agricultural science, and to the road-making side of engineering and aviation.

Now, in regard to lime in certain deposits, it is well known that calcareous weathering is not confined to any definite climate, but the lime horizon is taken as an important indicator in Soil Science. Care is required here. For example, Polynov states that calcium carbonate was not formed in the loess by weathering, but was introduced from outside, either during or after deposition.

From these studies, it is clear that the soil profile owes more to its historic climate than to that of the present-day, and that soil chemistry has much in common with the chemical aspects of the weathering process, which is an important branch of geomorphology.

Physical Problems cognate to Soil Science, Climatology and Geomorphology.

In the new soil science, great importance is attached to the physical properties, colour, texture and structure, and it is from these that a soil receives its type name. Now, soil is an assemblage of closed and open spaces, so that the movement of free air and free water through the soil becomes important. The wetting and drying of soil alters textural properties and also soil temperatures. The full appreciation of soil temperature and moisture must be related to climatic temperatures and moisture, and while climate is a study dependent upon its own measurable statistics, nevertheless the effectiveness of such a factor as rainfall must depend greatly upon soil character and soil temperature. Soil physics is therefore incomplete without this cognate study of climatology. Now soil physics and soil chemistry to a great extent become a study of colloidal clay content. Nevertheless, soils are classified as follows according to percentaged grain sizes: Coarse sand, 2–0·2 mm., fine sand 0·2–0·02 mm., silt 0·02–0·002 mm., clay less than 0·002 mm.

Prescott[12] has shown how texture may be estimated from mechanical analysis, and Weir's diagram[13] is somewhat similar (see Figs. 3 and 4).

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[11] Ibid., p. 183.

[12] Prescott, "Classification and Mapping of Soils", *A.N.Z.A.A.S.*, Vol. 23, Auckland, 1937, p. 260.

[13] W. W. Weir, 1936, *Soil Science*, p. 138.

It is generally considered that most agricultural soils would show a grain texture whose dimensions would fall into 2 mm. or less. We have examined a group of soils growing wheat and other agricultural crops in the Tamworth district, and shown that they would fall within the clay zone of the above triangle, though probably no soil surveyor in the field would place them in that category, since they contain too much sand and silt.[14] These soils, in addition, had gravel percentages bearing from 1% to 20%. Thus in field survey these Tamworth soils would be classed as sandy loams, but on mechanical analysis as clays and clay loams. Further, their structure in the field is materially influenced by the presence of gravel and small pebbles. Tamworth soils are not a special case, but typical of many of the soil regions of New South Wales.

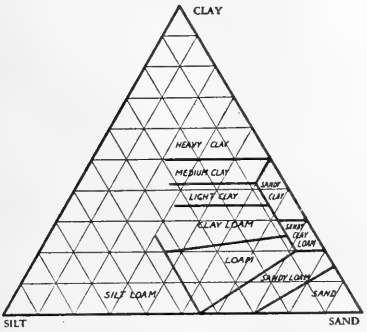

Fig. 3.—Correlation between the mechanical analysis of the soil and the estimate of the texture in the field. (After Prescott.)

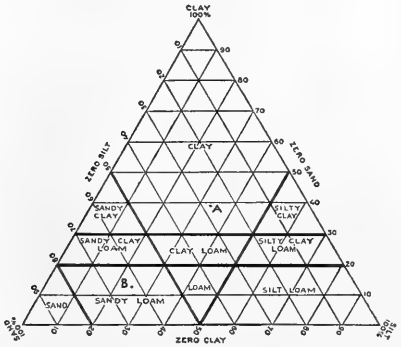

Fig. 4.—Triangle showing percentage composition in terms of sand, silt and clay. (After W. W. Weir.)

Again, over many of the hills of New South Wales a dark grey-black soil is found, associated with pebbles and even large boulders. In the Cassilis district, for example, boulders weighing from 20 to 100 pounds are embedded in clay so fine that after rain it is said to "melt away". These boulders and pebbles must play a large part in maintaining the continued immaturity of the soil, and are indicative of some cataclysmic agency in soil formation, rather than a disintegration of rock *in situ*.

It is right and proper that soil science should attain a degree of refinement such as is given by the Odén-Keen Balance, and yet it is imperative that the soil descriptions should permit of a simplified technique being carried out in field surveys, as is the case, and which is a further reason for a closer co-operation between geomorphology and soil science.

The movement of water in the soil must receive attention from a number of scientists, and many new and revolutionary concepts are being introduced. Much of the physics of the soil is therefore a study of the physical properties of soil moisture, and the following diagram by Hogentogler (Engineering Properties of the Soil, 1937), is appropriate (see Fig. 5). There is an interesting connection between the state of the soil and the amount and arrangement of the water in it. The diagram (see Fig. 6) illustrates one arrangement of the relation between the liquid, plastic and solid states and the moisture content and also illustrates the loss of volume of muck soil on drying. Again, civil engineers have a group

[14] W. H. Maze has shown me a light-weight soil growing excellent wheat which has 80% over 2 mm.

of studies called "soil mechanics". They have deduced many formulae connecting mechanics and soil; for example, the degree of instability of soil slope is deduced from the numerical fact that the profile of the surface of sliding always approaches the form of an arc, which is applicable to open soils but not to heavy clays. It has been shown that soils with little cohesion and in a loose state are liable to behave as a liquid and to flow on a horizontal surface, a feature which is related to the critical porosity of the soil.

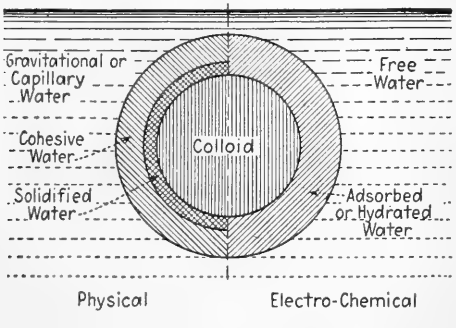

Fig. 5.—Types of soil moisture.

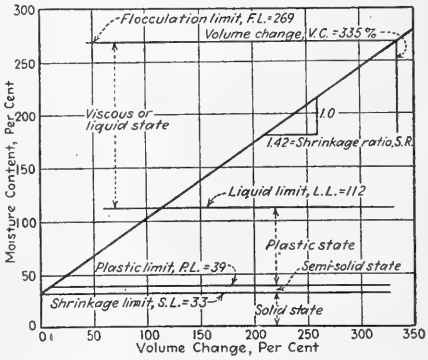

Fig. 6.—Relation between loss of moisture and loss of volume of muck soil on drying.

(Figs. 5 and 6 after C. A. Hogentogler.)

Many of the experiments in soil moisture content are of a laboratory character, but the conditions in the field are invariably very different. Soakage and seepage differ not only for different soils, but for different levels in the same soil. The artificial profile so often developed in agriculturally worked red soil often restricts water flow to the topmost portion, when it could be expected that lower horizons had become moist. We have repeatedly noticed the topmost zone of the profile to be moist, then followed by a dry and hardened zone, which in turn is followed by an almost liquid zone, which in a soil pit would immediately seep water. Again, percolation from a higher topographic level often has a marked change in the profile of soils considerably lower down. There is an interesting connection between infiltration capacity and moisture-retaining capacity, as the following examples (Fig. 7) show.

From these few examples it is fair criticism that any reasonably complete physical description of the soil in terms of Soil Science can only be complete when it is sufficiently fundamental, yet comprehensive enough to meet at least the ordinary needs of other sciences interested in soil.

Drift Morphometry and the New Soil Science.

Contemporaneous with the detailed study of soil samples in the laboratory there is a large-scale study of soil in the field, which, coupled with certain laboratory studies, has been described as "soil survey". Unfortunately, up to the present, soil surveys owe little to the application of geomorphological methods, though it has become clearly recognized in Soil Science that the infinite variety of soil types must be assembled into soil groups and categories. Furthermore, soil studies must play an appreciable part in any fundamental conception of the Universe as well as in economic world-harmony.

Geologists and agriculturalists are often reproached in that they have seen this soil science grow up almost without their aid. The reason, probably, is that the study of superficial deposits is possibly the hardest of all geological and geographical studies, though it is axiomatic that an interpretation of the past history of the earth is only to be found in present-day earth processes. Now the superficial covering of the earth's crust (including the soil) is not everywhere the same, nor is it an indiscriminate assemblage of the products of weathering. Soil and soil deposits are the end-point of denudation history, and as such group themselves into large entities capable of being recognized in the field. This fact has been appreciated in the Geological Survey of Britain, and geological surveys of several other countries, which have added to their solid Geology maps a series of Drift maps. These types of maps are fundamentally sound, whereas the unsatisfactory nature of the so-called "world soil groups" is due to the fact

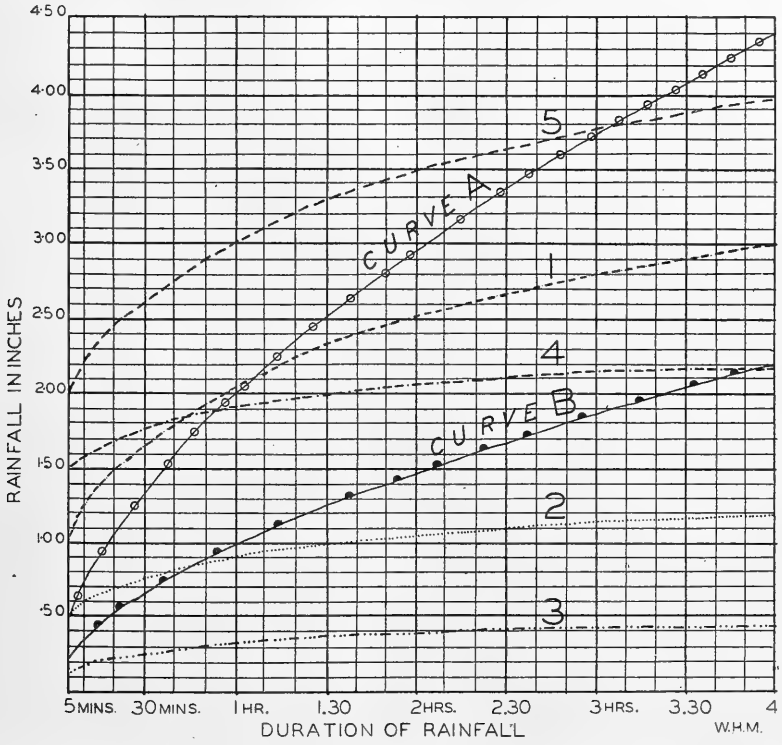

Fig. 7.—Measurements of Infiltration Capacity and Moisture-retaining Capacity.[15]
Curve A. Rainfall intensity which may be exceeded once in five years.
Curve B. Rainfall intensity which may be exceeded once in three years.

1. Infiltration capacity of dry soil at "Dalkeith".
2. Infiltration capacity of moist soil at "Dalkeith" (8 days after 1).
3. Infiltration capacity of wet soil at "Dalkeith" (2 days after 2).
4. Infiltration capacity 2, plotted above the one inch impounded by control measures.
5. Infiltration capacity 1, plotted above the one inch impounded by control measures.

[15] Holmes and Maze, University of Sydney Publications in Geography, No. 3, p. 6.

that they are an assemblage of convenience, possibly on the basis of least disadvantage, as much as an expression of the real surface covering of the earth.

Now, since soil deposits are the end-point of primary and secondary denudation history, it should be possible for the soil surveyor so to describe a profile that deductions could be made as to that denudation history, and the relation of past to present climate. From the fundamental character of the soil thus specified there could be chosen a boundary easily recognizable on the ground, and capable of simple insertion on a map. If it is true that deposits are entities, then there is here a pattern study over large areas, which must be capable of expediting soil mapping. It is not too bold to state that the expeditious mapping of drift deposits as an expression of the drifts themselves, and not in relation to their geological origin, would do much to advance the new study of Soil Survey.

Many drift deposits are of such great commercial value, e.g. brick clays, glass-making sands, foundry clays and sands, that a technique—a science—has grown up in connection therewith, and many of its analytical methods are the forerunners of those of Soil Science.

At the same time the study of superficial deposits is inadequate without reference to the historical factor, since these deposits are to be "read" like a palimpsest on which there are several superimposed "writings". While the earlier writing is recognizable, it is almost unintelligible in the present state of geological and climatological knowledge.

It is clear also that in many parts of the world the superficial deposits, which are co-extensive with soil, are not solely an expression of present-day denudation forces, but must include those of the Pleistocene or even earlier geological periods.

That there is a close connection between Soil Science and soil morphometry is illustrated from recent work in Australia. W. H. Bryan[16] examined the Red Soils of South-eastern Queensland from both aspects. From a study of the soil itself, he came to the conclusion "that the Red Earths were formed under an earlier climate, and one considerably different from that in operation at present, and that mild podsolization has been superimposed on them by the current pedogenic processes". Later he states that "the strictly geomorphic evidence is that the residuals occur as a distinct topographical feature inherited from an earlier physiographic epoch". . . . "This convergence of evidence fortifies one in the belief that the Red Earth Residuals may be regarded not merely as an interesting survival of an earlier landscape, but almost as a stratigraphical unit—a datum to which earlier and later evidence might be referred." Bryan would make them of Pliocene age.

Officers of the Department of Agriculture in New South Wales have examined similar Red Soils near Lismore, and find them something of a conundrum. On a brief visit to Lismore, I found that these soils are associated with basaltic flows not coincident in distribution, and each with different mineral content. Though the annual rainfall of the Lismore district is about 52 inches, podsolization (so-called) is very slight, but there is evidence (just outside Lismore) that a bright red soil was in existence between two flow episodes, and it has become hardened almost to a rock. These soils supported a dense, tall, forest vegetation of a semi-tropical type, but this "big scrub", as it has been called locally, has now almost been cleared to make way for paspalum grass pastures and dairy farms.

[16] Univ. Queensland, Department of Geology, Vol. i (New Series), 1939, No. 8.

Although there are lighter and darker soil types and a coastal greyer phase, all in a zone of heavy rainfall, there is extraordinarily little difference between the soil within the forest remnant and that outside under cultivation.

Again, Leeper, Nicholls and Wadham[17] have carried out a lengthy soil and pasture study in a dominantly basaltic area in Western Victoria. This study is a happy combination of modern soil technique with the methods of geomorphology. While there are the usual summation curves for mechanical analysis, and the characteristic chemical tables, the mineral aspect of the soil has not been lost sight of, especially in the expression of the silica content. For example, they find that the most striking feature of the minerals in the sand fractions is the abundance of non-basaltic materials, chiefly quartz, although the parent rocks of the district are of a basaltic nature. "This quartz, which is characterized by inclusions such as rutile and zircon, and which appears rounded and water-worn, could not have crystallized from the basaltic magma, and the grains of zircon, tourmaline, andalusite, etc., which are associated with the quartz, obviously represent foreign material. The most likely source of this material is the volcanic ash, since, as has been stated, the explosive rocks of Mt. Gellibrand contain considerable percentages of included quartz and other non-basaltic minerals, and the proportion of these foreign minerals was probably higher in the fine material which fell over the plains."[18] But it is also stated that much of the fine sand in this area has been added by the wind. Again, they show that there are remarkable changes in the sandiness with depth, one example "showing a percentage of 26 at the surface to a minimum of 14 at two feet, and rising again to a second maximum of 23 at three feet".[19]

Another type of study is that of Milne,[20] who states that "the language of soil description lacks a suitable term having a cross-country dimension, and the want of it is felt as soon as soils are discussed in relation to the lie of the land, as in this matter of erosion. To help in such discussions the word *catena* has been adopted (Provisional Soil Map of E. Africa, 1936) to describe a topographic complex of soils such as is represented in my example". He describes a zone distribution of soil types in relation to topography, and the diagram (see Fig. 8) herewith is sufficient for the present exposition.

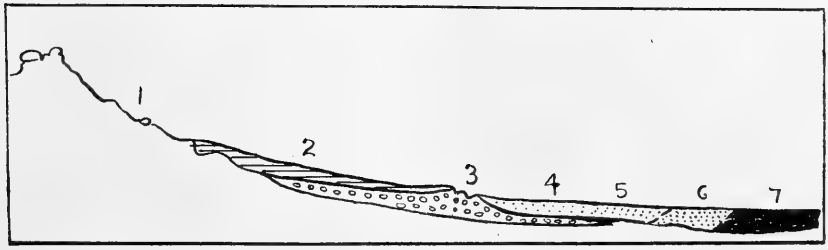

Fig. 8.—Soil catena. (After Milne.) 1, Shallow skeletal dark grey loam; 2, Deeper soil of Red Earth group; 3, Coarse granitic grit in black and rusty ferruginous cement; 4, washed sand; 5, 6, Silty or clayey sand; 7, Level clay floor.

[17] "Soil and Pasture Studies in the Mount Gellibrand Area, Western District of Victoria", *Proc. Roy. Soc. Vict.*, xlix, Part i, 1936.

[18] Ibid., p. 111.

[19] Ibid., p. 113.

[20] *Nature*, Vol. 138, Sept. 26, 1936.

In Eastern Australia similar complexes are recognizable, but they are complicated still further with the effect of Pleistocene sub-antarctic climate.

In the recent Proceedings of this Society (1937, Vol. lxii, in Parts iii and iv) I drew attention to the significance of slope-site and situation factors in soil description. In New South Wales the distinctive soil types are closely related to their topographic site, and the conditions of their accumulation. Red Loams are found in favourable middle-slope soils, and heavy clays in an intermediate position, derived from the ponding back of flood-water.

While grey soils are characteristic of high hills in New South Wales generally, there are several wide zones of black soils, with a deep brown B horizon, not precisely related to basalts, and equally wide plains with comparatively shallow black clay soils, most of which must have come from the neighbouring though far-away hills, and been re-sorted in the still waters of shallow lakes.

The discussion of pedogenic processes has been too theoretical. Even Robinson, in "Soils, their Origin, Constitution and Classification",[21] pays little attention to geomorphology. There has been a too elemental assumption that soil is formed directly from an immediately underlying parent rock. Rarely is this precisely true, except in topographic situations, not always at high elevation, where erosion has been intense, and/or where primary igneous rocks outcrop. Most sedimentary rocks, some limestones and mudstones, and even many metamorphic rocks are repeated assemblages. They have been the products of some past erosion cycle, but are now beginning their soil-forming history, wherein the stages of weathering are well advanced.

Of the three stages in denudation, namely, disintegration, transportation, and deposition, the last two play major parts in soil-making. The products of disintegration over many rock types are thus transported, as a whole, long distances, and undergo much re-sorting and re-shuffling. There are cataclysmic mass movements, like landslides and subsidences, and their lesser manifestations in terracettes: also slow and sometimes imperceptible movements like soil creep and soil shrinkage. Further, there have been, in the recent past, movements of slow flowage, which greatly determine the present-day source-material of soils.

Now, soil creep shows itself in the profile as a banded arrangement. Often there is an important stone-line, but a distinction must be made between stone-lines due to creep and stone-lines due to repeated deposition. Creep appears on a large scale in forested country and in grassland pastures, and especially in high country where frost is prevalent, but occurs even on gently sloping country, due to marked seasonal wetting and drying and marked temperature changes. This summer, for example, right through the northern central parts of the State, there is evidence in wide cracks and minute slumping that there has been considerable creep downhill, a feature which is likely to be accelerated when the autumn rains set in.

Closely related to the problem of soil creep are the problems of soil shrinkage. There is the well-known deep cracking of black soil, but in the Red Loams cracking is equally prevalent, especially in periods of severe drought. Complete drying out of the soil profile leaves wide cracks, which, coupled with the absence of vegetation, allow a large amount of sand and coarse material to be wind-blown into them, which ultimately penetrates far into the readjusted soil profile. It must be realized that these cracks may be several inches wide and several feet deep. One of the most spectacular examples of shrinkage was shown after the

[21] Thomas Murby and Co., 1936.

drainage of the English Fenlands, where it has been claimed that a drop of 15 feet took place when the soil profiles dried out.

The heaving of soil under frost action presents many problems, especially to road-makers, but has been taken advantage of by farmers, who plough stiff land before the winter, allowing the frost to break it down into a fine tilth. Conversely, the recognition of former soil surfaces in deposits not now experiencing movement accounts not only for the origin, but also for the present character, of the surface soil. The significance of the wide expanse of Red Soils, of the parallel sand-ridges in the great Sand Ridge Deserts, of the so-called Mallee soils, and of the extensive stony plains soils, all surface forms so characteristic of very much of inland Australia, will become apparent by methods of soil-deposit profile analysis, while they would yield little or nothing to a soil analysis. Dr. Madigan[22] has described very ably the parallel sand-ridges of the Simpson Desert, and correlated them with the present-day prevailing winds. One meets with sand ridges in many parts of Australia, outside their chief localities, and an examination of their marginal, rather than their central, phases, is likely to yield the most significant results.

The cross-section of a parallel type sand-ridge shows two aspects, a lower and hardened red sandy zone, occasionally with calcareous nodules, and an upper and lighter zone, wind-fretted at the surface. Madigan has stated that the sand of the sand ridges moves longitudinally. My brief examination of a few central Australian ridges, and a flight across part of the Simpson Desert, confirms my earlier observations on sand ridges, that the sand only moves longitudinally because it is forced by lateral winds in a sigmoid fashion along the ridge, a phase which suggests a new development on the older and underlying part of the ridge. The opinion can be expressed that the upper and lower parts of the ridge show two separate morphologies, not strictly coincident. The term "palingenesis" could be applied here, as in other branches of science, for sand-ridge topography in Australia is not strictly present-day, and many of the topographical characteristics are inherited. This becomes evident if other deposits in inland Australia, cognate to the sand ridges, be examined.

The enormous extent of stony gibber plains has excited interest. These present-day loose deposits are generally considered to be derived from duricrust, but their present *lie* permits of additional explanations.

Now gibber or stony plains, seen from an aeroplane, exhibit distinctive patterns, and crests of lightly coloured stones show up like the crescentic waves of a trade-wind sea. A popular name for some of the areas is "Bay of Biscay" country, because of the jolting that a rider or motorist experiences in crossing them. These extensive stony plains are carpets of loose stones, almost always bare of vegetation. The stones are of all sizes, some well-worn and desert-polished, while others appear as if just fresh from a recent rock out-crop. The whole mass is obviously a reassemblage of very ancient and very modern products of weathering. Among the stones is a very fine matrix of red sand and calcareous silty clay. Immediately after rain, the whole surface becomes impassable, because of its soft character, and one is as easily bogged on this stony surface as on the notorious black soil. On some gibber plains, of course, the deposit is very shallow and the motoring surface correspondingly harder. Now the pattern of the larger stones, as stated, is obvious from the air, but even when seen from ground level there are polygonal shapes and long stone stripes. These are especially noticeable

[22] "The Australian Sand-Ridge Deserts", *Geog. Review*, xxvi, No. 2, April, 1936.

on the stretch south of a line from Oodnadatta to Ernabella, and south of the Western Macdonell Ranges on areas several miles from rock outcrops, though these gibber zones are obviously related to the flat-topped quartzite-capped central Australian mesa topography.

Now this "Bay of Biscay" country, with its stone polygons and stripes, could only come about by intensive weathering and much re-sorting, due to a slow flowage of the deposit as a whole. It is possible that the intermittent and occasional heavy rainfall of Central Australia, occurring on these long, gentle and somewhat convex slopes, would permit of such a re-sorting of the deposit. But desert rainfall is not always torrential, though on occasions enormous volumes can reach the creeks, as is shown by the extraordinary spate of the Finke and Algebunga, and the filling of Lake Eyre in 1938/39.

This type of re-sorted stone-patterned landscape, however, has been considered to be associated principally with cold climates, and especially climates with large quantities of slowly melting snow, where there is no appreciable run-off at the surface but an abundance of water throughout the surface deposits.

As far back as 1906, the term "solifluction" was used for a rock debris landscape in which the rock flowed as a whole.[23] Again, Huxley and Odell[24] describe a series of surface markings in Spitsbergen, e.g., stone polygons and arcuate markings, and it seems to be quite clear that all these re-sorted stone patterns represent a relatively stable phase in the weathering of certain types of arctic surfaces. However, it would appear that the stone polygons are a temporary phase in sub-arctic lands, and it is suggested that "it might conceivably be possible to obtain some idea of the time a country has emerged from glacial conditions by the condition of its stone polygons".

Recently stone stripes attributed to frost heaving have been described in the northern part of the Lake District in England. Again, it may be that the slow seepage of widespread rainfall over a very large and gently-inclined catchment area, as in central Australia, may produce re-sorting of bare deposits into patterns analogous to those of snow climates like that of Spitsbergen.

However, I am of the opinion that these central Australian stony deposits show evidence of cold sub-antarctic climate in central Australia in Pleistocene or Post-Pleistocene times. I want to make it quite clear that, while glaciations have been described for central Australia in pre-Cambrian and probably Cretaceous times, for which there is ample geological evidence,[25] this loose gibber deposit is in great part a fossil deposit, with stones of pre-Cambrian, pre-Cretaceous and Cretaceous times and of the present day all grouped together.

If the extent of Pleistocene glaciation is to be measured by the Kosciusko type, then moraines and other deposits characteristic of glaciated country are not to be expected in central Australia. Nevertheless, if there is anything in the climatic theory of soil formation, and if the soil deposit profile becomes an indicator of past climates and past denudation history, then these inland stony deposits are consequent upon sub-antarctic climates; and further, these stony plains and the parallel sand-ridges are cognate landforms.

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[23] *See* W. H. Hobbs, *Mex. Acad. Sci. Annual Report*, 1910; W. E. Ekblaw, *Proc. Nat. Acad. U.S.A.*, 4, 1918.

[24] *Geographical Journal*, lxiii, 1924, 207.

[25] W. G. Woolnough and Sir T. W. E. David, "Cretaceous Glaciation in Central Australia", *Quart. J. Geol. Soc.*, lxxxii, Part 3; E. C. Andrews, "Geology of Broken Hill District", Department of Mines, *Mem. Geol. Surv. N.S.W.*, No. 8.

It is worth examining these superficial deposits further, for there is an urgency in Australia for a correlation of Pleistocene and post-Pleistocene landforms. There are, for example, (i) certain deposits which are the result of equiplanation, (ii) the recent valley-in-valley structure so prevalent in New South Wales, (iii) the fact that many tributary streams are concordant only with former flood levels, (iv) the headwater slumping of many deep deposits now fairly stable, and (v) the recent rejuvenation of erosion, perhaps only in part man-made.

Jensen, in his survey of the Walloon Beds in the Carnarvon Range, Queensland,[26] describes certain remarkable boulder mounds. "The . . . explanation is that these boulder mounds are of glacial origin. Although in several places in the Injune Valley they closely resemble moraines, the facts of their distribution suggest rather deposition by floating icebergs which became stranded on the shores of the Late Cretaceous sea. There may have been isolated islands with rhyolite cappings which were scoured by these bergs and yielded them material to dump elsewhere."

"This theory explains why large areas of blacksoil plain are entirely free from boulders, while right in the midst of them are boulder patches forming little hills. The glacial theory also helps to explain the wide distribution of boulders and gravels over the Cretaceous at Roma and further west at Longreach. In the latter area granite, porphyry, quartz, and topaz belonging to country hundreds of miles distant form gravel areas which are a source of mystery on our western plains."[27]

Jensen also considers the boulder mounds to be older than a basaltic phase. In view of the relation of these boulder zones to the basalts I would hazard the opinion that they are related to the time of the gravel deposits known as "deep leads" in New South Wales, and usually related to Tertiary times.[28]

Not everywhere are gravel deposits, like the "deep leads", covered with basalts. There are several examples in New England which are soil deposits of to-day, yet their mineralogical character and distribution make them contemporaneous with the "deep lead" deposits.

Now many hill-tops in New England are of basalt underlain by gravel, which in turn is underlain by granite. It is customary to consider most of that area as composed of granitic soils, but the long gentle slopes, sometimes in pasture and sometimes under the plough, show a mixture of conglomeratic gravel and basaltic and granitic rock debris. Hardly anywhere in New South Wales, except in small areas, is there a simple soil profile; even in many areas on the Hawkesbury sandstone around Sydney there are patches of Wianamatta shale. It is a direct inference that sandstone soils, so-called, are frequently shale-enriched.

The study of Pleistocene deposits in Europe has become important, especially in regard to the early history of man. In Europe, glacial conditions left behind well-recognizable boulder-clays with interglacial deposits. In most of the horizons, palaeological industries have been discovered. In Australia mammalian fossils

[26] Jensen, "Geological Reconnaissance between Roma, Springsure, Tambo and Taroom", *Qd. Geol. Surv. Publ.*, No. 277, 1926.

[27] Ibid., p. 39.

[28] Dr. Walkom, in private conversation, stated that from examination of the fossil leaves in certain of these deep-lead deposits, difficult though that kind of evidence is, the summation of evidence points to the deposits being Tertiary. Nevertheless, Jensen's boulder mounds may relate to a more recent glacial period than Cretaceous. Professor W. R. Browne, in a conversation, considered that there are two sets of "deep-lead" deposits of different ages.

have been found, and it may yet be possible to discover in the post-Miocene deposits of Australia evidences of the earliest aboriginal occupancy of the Australian continent.

One further case may be cited in this brief description, that of what I call the Menindee Sand Deposits. Around the River Darling, in the neighbourhood of Menindee, for forty miles to the east and ten miles to the west, there are filled-in flood channels and sand-hills, which may rise to 20 feet. The floods of historic time have been shallow and widespread, and have taken no part in the creation of these deposits. (I have been fortunate in having been in that area during two floods.) The inference is that the Darling and its distributaries must have occupied a level at least 20 feet higher than to-day, and at full flood must have covered an area comparable to an inland sea. Indeed, the aboriginal belief of a great inland sea in New South Wales may support that contention. The Menindee Lakes, for example, some of which are 30 by 20 miles, and surrounded by high sand-hills, are obviously very recently filled-in river channels, and the sand-hills are derived from a deltaic deposit on their banks. The sand-hills throughout this area are very stable, and the diagram (Fig. 9) illustrates the present and recent topographic forms. The so-called Australian group of Mallee soils, which lie to the south of the Menindee deposits, will eventually be related to this phase in the history of the Darling River.

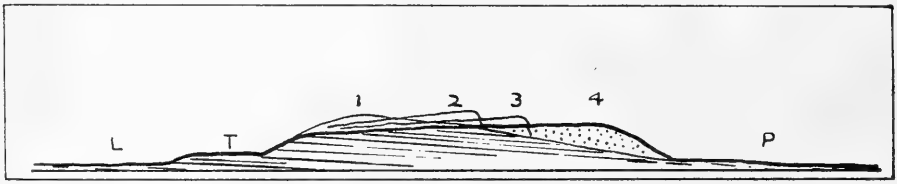

Fig. 9.—The Menindee lake deposits and the recent formation of the sandhills. L, edge of lake bed; T, a small terrace; P, red sandy plain; Shaded area, total body of river silt; 1 to 4, stages in scouring to form sandhills.

On the point of sending this to the press, there comes to hand an excellent paper by Dr. Dorothy Carroll.[29] Though I do not think Dr. Carroll's investigations have exhausted the soil questions in the west, the following paragraphs from her conclusions are very pertinent to my argument:

> "From field evidence it appears that the sand-plains are true sandy soils of a fossil or residual character, owing their formation to some process not now in operation." . . . "Therefore in this part of Western Australia there are two distinct periods of soil formation: present-day soils, normal red to reddish brown loams and clays in the more low-lying parts formed by weathering *in situ* of the country rocks (some of these soils have suffered slight local transport); and old soils—the yellow to pale brown sands of the plains containing a lateritic layer which the other soils do not. The sand-plains are residual and are preserved to-day because of the low relief and scanty rainfall of this part of the country."
>
> . . . "The idea that the sand-plains are soils overlying granite has been widely accepted and has much more foundation, for granite and gneiss do underlie many parts of these plains; and until a mineralogical examination

[29] "Sand-plain Soils from the Yilgarn Goldfield", *Bull. Geol. Surv. W. Aust.*, 97, 1939.

had been made no one who believed in the sedentary character of the sand-plains had suggested that any other rock but granite might give rise to a sand-plain. Modern soils developing in the more low-lying parts of the district vary according to the under-lying rock. Occasionally in some of the sand-plain areas we find granite outcrops surrounded by newly-formed pinkish brown soils. These soils are not at all similar to the yellow soils of the sand-plains themselves, and this suggests that the normal weathering of a uniform expanse of granite could not, under the present climatic conditions, give rise to the typical sand-plain. Another feature of importance is the absence of a lateritic layer in the modern soils, whereas it is a constant feature of the sand-plain soils. The sand-plain soils must therefore be residual, and the second suggestion, that they are normal granitic soils, is also dismissed, leaving only the third possibility (fossil soils) which has been proved to be correct by the result of this investigation."

The conclusions I want to draw from these morphometric studies of soil deposits are as follows:

(i) That most of the soils (in the narrow sense) in New South Wales, and in several other parts of Australia, are being formed from superficial deposits.

(ii) That these deposits, though widespread and though of greatly mixed mineralogical character, can be related to past and present cycles of denudation history.

(iii) That deposit morphometry is a primary study in the new Soil Science and in soil mapping.

Consequential Studies of Soil Science.

The new soil science is no longer a farmyard study, and, as Prescott says, a discussion of pedological matters "may be so far removed from those of agriculture and forestry as to raise doubts as to whether it can be rightly treated as a subject of interest to an agricultural section at a meeting of the Association for the Advancement of Science".[30] The same could be said to be true of deposit geomorphology, because most of the work has been done by engineers and officers attached to such services as the Soil Conservation Service. Indeed, there is need for coordinating a technique which will give us a description of soil and soil deposit profiles adequate for the soil scientist, the geomorphologist, the agriculturalist and the engineer. The new need for soil knowledge in these applied studies may cause them to outstrip the old-established scientific departments, and even the newer Soil Science. The Soil Conservation Service of the United States, for example, required a reclassification of soils, especially in terms of soil movement potential, before there could be carried out their rehabilitation projects and their national surveys of land utilization.

Again, under natural conditions, changes in the soil profile and in the soil deposits are comparatively slow, but under systems of de-forestation, pasture improvement, and intensive agriculture, the tendency for soil movement and for elaborate profile changes becomes great. Under these conditions, it is doubtful if a soil type, based on purely surface phenomena, and even when well established, is likely to persist for long. For these reasons, the order of accuracy necessary in Soil Survey is not as great as in Geological Survey or in a precise topographic survey, nor indeed as great as in Soil Science itself.

[30] Prescott, "The Classification and Mapping of Soils", *A.N.Z.A.A.S.*, Vol. 23, p. 258.

Again, there are (i) the large-scale soil problems connected with very frequent and extensive bush-fires, seemingly inseparable from human activity, (ii) the problems of soil change in Australia from a forest to a grassland environment, (iii) the mechanical soil depletion due to ruthless agricultural methods, and (iv) the equally important vicious depletion, because not seen, of the plant-food chemicals of the soil, due to lack of refertilization. It has become axiomatic that the more fertile the soil, the lower the standard of living. The soil problem is immediately of a grave sociological character.

It is sufficient to realize that soils (in the wider sense) and soil-forming processes are regional, but that land tenures and soil-usage methods are local and individual. Almost every land problem is regional as the land-utilization revolutions in America and Russia show. There are such great social limitations imposed by varying soil types, divergent areal fertility and effective probable rainfall that to bridge the gap between enforced individual exploitation of the soil and land husbandry there is required either a very elaborate co-operative effort among local land users or a major political recasting of the local and national responsibilities of farmers and pastoralists.

I do not propose to follow these thoughts any further at present, as I have already done so elsewhere.[31]

Yet it were well if I left you with this diagram (Fig. 10), which is almost self-explanatory, to complete the sequence of ideas on the Science of the Soil.

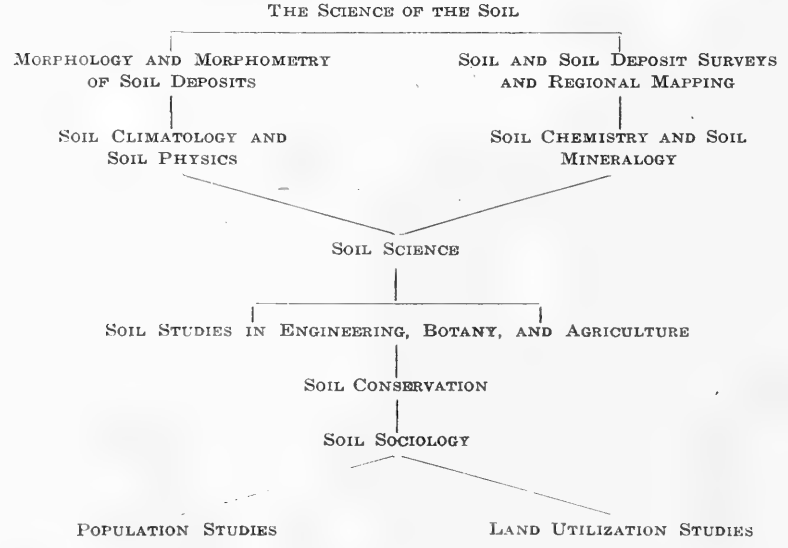

Fig. 10.—Diagrammatic representation of the sequence of studies in the Science of the Soil.

[31] *Univ. Sydney Publ. in Geography*, Nos. 1 and 2. The following books are to the point: S. M. Wadham and G. L. Wood, "Land Utilization in Australia", 1939; Bank of N. S. Wales Circular, 1939, Vol. ix, No. 1, "The Depreciation of Soil Productivity"; Report of Soil Erosion Committees in South Australia and in Victoria, 1938; "The Soil and its Influence on American History", A. B. Hulbert, 1930; The Soil Conservation Act, 1938, N. S. Wales.

The Secretary, for the Honorary Treasurer, presented the balance-sheets for the year ended 29th February, 1940, duly signed by the Auditor, Mr. F. H. 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 Chairman declared the following elections for the ensuing session to be duly made:

President: R. H. Anderson, B.Sc.Agr.

Members of Council: R. H. Anderson, B.Sc.Agr., Professor W. J. Dakin, D.Sc., R. N. Robertson, Ph.D., B.Sc., H. S. H. Wardlaw, D.Sc., G. A. Waterhouse, D.Sc., B.E., F.R.E.S., W. L. Waterhouse, M.C., D.Sc.Agr., D.I.C. (Lond.), A. R. Woodhill, B.Sc.Agr.

Auditor: F. H. Rayment, F.C.A. (Aust.).

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

Linnean Society of New South Wales.

GENERAL ACCOUNT. Balance Sheet at 29th February, 1940.

LIABILITIES.	£ s. d.	£ s. d.
Capital: Amount received from Sir William Macleay during his lifetime	14,000 0 0	
Further sum bequeathed by his Will	6,000 0 0	
		20,000 0 0
Contingencies Reserve		9,315 16 1
Commercial Banking Coy. of Sydney, Ltd.		286 0 9
Suspense		0 7 10
		£29,602 4 8

ASSETS.	£ s. d.
Society's Freehold	11,000 0 0
Australian Consolidated Loans, Bonds	500 0 0
Loans on Mortgage	2,500 0 0
Science House (one-third share)	14,590 0 0
Metrop. W.S. & D. Board Debentures	494 7 6
Rural Loan	386 0 0
Cash in hand	10 0 0
Income Account	121 17 2
	£29,602 4 8

INCOME ACCOUNT. Year Ended 29th February, 1940.

	£ s. d.	£ s. d.
To Balance from 1938/39		45 9 1
„ Salaries		1,010 0 0
„ Printing Publications	681 17 6	
„ Illustrations	93 16 11	
		775 14 5
„ Rates and Insurance		187 15 10
„ Library		15 4 7
„ Postage	45 9 10	
„ Petty Cash	13 9 1	
		58 18 11
„ Audit	7 7 0	
„ Printing	18 5 3	
„ Expenses	19 12 9	
„ Attendance and Cleaning	35 19 2	
„ Grants	20 0 0	
		101 4 2
„ Bank Expenses		1 17 10
		£2,196 4 10

	£ s. d.	£ s. d.
By Subscriptions: 1939/40	157 10 0	
Arrears	14 14 0	
In Advance	5 5 0	
Associate	0 10 0	
		177 19 0
„ Entrance Fees		7 7 0
„ Donations for Printing		214 9 6
„ Interest		176 14 6
„ Rent		338 0 0
„ Science House		260 0 0
„ Sales (including 60 copies of PROCEEDINGS purchased by Government of N.S.W.)		185 7 8
„ Fellowships Account (surplus income at 29th February, 1940, transferred)		714 10 0
„ Balance to 1940/41		121 17 2
		£2,196 4 10

Examined and found correct. Securities produced.
F. H. RAYMENT, F.C.A. (Aust.),
Auditor.
Sydney, 14th March, 1940.

G. A. WATERHOUSE,
Hon. Treasurer.
7th March, 1940.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

BALANCE SHEET at 29th February, 1940.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.
Amount bequeathed by Sir William Macleay ..	35,000	0	0	Australian Consolidated Loans, Bonds	10,400	0	0
Surplus Income Capitalized	15,539	17	0	Loans on Mortgage	38,139	18	9
				Rural Loan	477	10	0
				Metropolitan W.S. & D. Board Loan	1,005	0	0
				Commercial Banking Company of Sydney, Ltd. ..	407	11	3
				Commonwealth Savings Bank	109	17	0
	£50,539	17	0		£50,539	17	0

INCOME ACCOUNT. Year Ended 29th February, 1940.

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	1,348	14	4	By Interest	2,314	10	0
„ Capital Account	251	5	8				
„ General Account	714	10	0				
	£2,314	10	0		£2,314	10	0

Examined and found correct. Securities produced.
F. H. RAYMENT, F.C.A. (Aust.),
Auditor.
Sydney, 14th March, 1940.

G. A. WATERHOUSE,
Hon. Treasurer.
7th March, 1940.

BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 29th February, 1940.

LIABILITIES.	£	s.	d.
Amount bequeathed by Sir William Macleay	12,000	0	0
Accumulated Income Capitalized	3,820	0	0
Income Account at 29th February, 1940	1,472	14	4
	£17,292	14	4

ASSETS.	£	s.	d.	£	s.	d.
Australian Consolidated Loans, Bonds				15,820	0	0
Cash—						
Commercial Banking Company of Sydney Ltd.	227	13	7			
Commonwealth Savings Bank	1,239	0	9			
In hand	6	0	0			
				1,472	14	4
				£17,292	14	4

INCOME ACCOUNT. Year Ended 29th February, 1940.

	£	s.	d.
To Salaries	687	10	0
„ Expenses	11	18	9
„ Petty Cash	2	14	4
„ Balance to 1940–41	1,472	14	4
	£2,174	17	5

	£	s.	d.
By Balance from 1938-39	549	17	8
„ Interest	624	19	9
„ Donations for Assistant to Bacteriologist	400	0	0
„ Donations for Plant House	600	0	0
	£2,174	17	5

Examined and found correct. Securities produced.

F. H. Rayment, F.C.A. (Aust.),
Auditor.
Sydney, 14th March, 1940.

G. A. Waterhouse,
Hon. Treasurer.
7th March, 1940.

CONTRIBUTIONS TO THE NITROGEN ECONOMY OF AUSTRALIAN WHEAT SOILS, WITH PARTICULAR REFERENCE TO NEW SOUTH WALES.[1]

By H. L. Jensen, Macleay Bacteriologist to the Society.

(Plate i; five Text-figures.)

[Read 27th March, 1940.]

Contents.

Introduction.

Wheat is the most important cereal crop of Australia. The area devoted to its cultivation steadily extended until about 1930, and has for the last decade averaged about 14 million acres, or nearly two-thirds of the total area under cultivation. This wheat area gives an average annual harvest of about 160 million bushels, of which nearly 30% has been produced in New South Wales. The area under wheat for grain in this State has since 1926 averaged about 4 million acres, with an average annual production of about 51 million bushels; the average yield per acre is thus approximately 12·6 bushels. The southern parts of the wheat belt (Riverina and South Western Slopes) in New South Wales contain most of the wheat area.[2]

[1] Approved as a thesis for the degree of *Doctor agronomiae* in the Royal Veterinary and Agricultural College, Copenhagen.

[2] Detailed figures in The Official Year Book of Australia, No. 29—1936, and The Official Year Book of New South Wales, 1935-36. Here also description and map of the wheat belt of New South Wales. Prescott (1934) gives a general survey of the extent and character of the wheat belt in Australia.

The yield of wheat is closely correlated with the rainfall. In South Australia, Prescott (1934) calculated a close and positive correlation between yield per acre and mean rainfall from April to November, and in New South Wales the most fertile wheat districts are found on the Western Slopes in the southern parts of the State, where the average annual rainfall is about 25 inches, with a maximum in winter. Nevertheless the breeding of drought-resistant varieties has made it possible to grow wheat profitably, although with a much lower yield per acre, in districts where the rainfall is as low as 9 or 10 inches.

The common practice in New South Wales is to grow wheat alternating with fallow, or else to interpose a crop of oats for grain, hay or grazing, after the wheat crop. Sowing of the wheat normally takes place in April–May, and harvest in November–December. In harvesting, the heads of the wheat are usually stripped off and the straw burned, either immediately after harvest or else in February–March. The subsequent fallow may be "short", i.e., the ground is ploughed immediately after harvest and stubble-burning, kept bare until May, and then sown with wheat again (common in the northern districts where most of the rain falls during the summer), or "long", i.e., the stubble-ground is not ploughed until the autumn rains begin in May–June, and is then kept bare until sowing-time next year. This is common in the southern districts with winter maximum of rainfall. Spontaneously appearing herbage on the stubble fields is often grazed by sheep, before the fields are ploughed in the autumn. In South Australia and Victoria the wheat or oats crop is often followed by one or two years of pasture, and the stubble-burning may be omitted. This practice is also sometimes followed in New South Wales. Not infrequently the fallowing is omitted and wheat is sown directly on ploughed stubble-land, but as a rule this gives lower yields than sowing after fallow.

It has long been recognized that phosphatic fertilizers regularly improve the yields in the principal wheat-producing areas of Australia, but nitrogenous fertilizers have usually been found to have little or no effect. [Data from earlier experiments in Victoria have been collected by Howell (1911), and more recent data are quoted by Prescott (1934).] In South Australia, Richardson and Fricke (1931) and Richardson and Gurney (1934) found profitable responses from the application of ammonium sulphate or sodium nitrate to cereals sown on stubble land, but not after fallow; they ascribed this difference to the higher nitrate content of the fallowed land. Prescott (1934), in a discussion of the value of fallowing, concludes that the production of nitrate may be more important than the conservation of moisture, to which the good effects of fallowing are often ascribed. In practical wheat farming nitrogenous fertilizers are never used. Since the average nitrogen content of Australian wheat is a little less than 2% and the average weight per bushel some 62–63 lb., the average 12·6-bushel crop in New South Wales thus carries away between 14 and 15 lb. of nitrogen, in the grain alone, from each acre of land. With allowance for the loss of nitrogen caused by stubble-burning, we must reckon with an average consumption of at least 20 lb. of nitrogen per acre per wheat crop, so that the 4 million acres of wheat land in New South Wales annually lose nearly 35,000 tons of nitrogen. To this must be added further quantities represented by the production of oats and of wheaten hay,[3] as well as the nitrogen involved in the production of wool and meat by sheep grazing on the stubble fields.

[3] Wheaten hay is in New South Wales annually grown on an area of about 300,000 acres, with an average production of 1·2 tons of hay per acre.

Unless compensated in some way, this continued removal of nitrogen in the crops must represent a heavy drain upon the nitrogen reserves of the soil, which are not very large in most of the typical wheat areas. Apart from limited areas of heavy black and brown basaltic earths of an almost chernozem-like character in Queensland and northern New South Wales, there are probably few wheat soils that contain more than a few per cent. humus and 0·1 per cent. total nitrogen.[4] Already Howell (1911) has emphatically pointed out the dangers of soil exhaustion by continued wheat cultivation without compensation for the plant food taken away. From the fact that wheat has in some districts been cultivated on the same land for 50–60 years and even more without nitrogenous fertilizers and without any apparent decline in crop yield (as it has been in India for centuries), one might indeed be inclined to conclude that some natural factor compensates the land for the continual removal of nitrogen. But if this is not the case, the nitrogen requirements of the crops must wholly or partially be met by conversion of a part of the humus nitrogen into plant food. This involves a gradual destruction of the humus, eventually leading to unproductiveness and possibly having a close connection with the phenomenon of soil erosion, which in recent years has assumed alarming proportions, not least in the wheat districts. There is therefore an imperative need for a detailed examination of the various factors that influence the nitrogen balance in the wheat soils.

If we leave out of consideration the still unconfirmed statement by Lipman and Taylor (1924) that the wheat plant itself is capable of fixing nitrogen, as well as nitrogen fixation by trees and bushes (Ericaceae, Elaeagnaceae, Casuarineae, etc.), which do not occur on the wheat fields, we have the following natural factors known to be able to add combined nitrogen to the soil:

(1). Rainfall, which brings down small quantities of nitrogen, chiefly nitrogenous oxides produced by electric discharges in the atmosphere;

(2). Nitrogen fixation by leguminous plants, wild or cultivated;

(3). Nitrogen fixation by free-living soil microorganisms.

A fourth factor might be represented by nitrogen fixation through physico-chemical agencies in the soil (Warmbold, 1906; de' Rossi, 1932*c*; Dhar, 1937). The existence of these phenomena, however, still remains to be proved.

The third factor—nitrogen fixation by free-living organisms—has often been considered highly important in soils from warm and arid climates [for references, see Russell (1937); cf. also Kostytchev (1924), Lander and Ali (1925), and Gainey (1932)]. In the interior of New South Wales the rate of evaporation of water practically everywhere exceeds the rainfall except for limited periods in winter time in certain districts; the climate is thus predominantly arid.[5] The process of non-symbiotic biological nitrogen-fixation therefore deserves careful study as a link in the nitrogen problem of the wheat soils of Australia. To undertake such a study on systematic lines has been the scope of the present work. When this was started towards the end of 1935, there were in the literature only few contributions dealing with the occurrence of nitrogen-fixing bacteria in Australian soil and practically no experimental work had been done on the quantitative aspect of this problem.

[4] Detailed descriptions of the soil types of Australia in general, and New South Wales in particular, are due to Prescott (1931) and Jensen (1914).

[5] Official Year Book of New South Wales, 1935-36. Cf. also Richardson (1923) and Richardson and Fricke (1931) on rainfall and rate of evaporation in Victoria and South Australia.

The Microorganisms Active in Non-symbiotic Nitrogen Fixation.

The investigations of Berthelot (1888–90) from 1885 onwards were the first to deal rationally with the problem of fixation of elementary nitrogen by microorganisms not living in symbiosis with a host plant. Although it may nowadays, as pointed out by Waksman (1932), appear open to doubt whether nitrogen fixation actually took place in Berthelot's experiments, these investigations proved highly fruitful by stimulating interest in the problem, and opened up an ever-increasing flow of contributions to the problem of microbial nitrogen-fixation.

The microorganisms capable (or allegedly so) of fixing elementary nitrogen without symbiosis with a host plant are:

1. *Aerobic organisms.*—The most important group of these is the bacterial genus *Azotobacter*, first discovered by Beijerinck (1901). The genus includes four well-defined species, *Az. chroococcum*, *beijerinckii*, *vinelandii*, and *agile*, of which the first is by far the most common in the soil. A fifth species, *Az. indicum*, has recently been added by Starkey and De (1939).

The group has been studied very thoroughly from different angles,[6] and in recent years Burk and co-workers (1930–36) have given numerous important contributions to its physiology. The main points may be summarized thus: The *Azotobacter* are strictly aerobic organisms, although still capable of growth at quite low oxygen tensions (Meyerhof and Burk, 1928). Their temperature range extends from about 10°C. to about 40°C., with an optimal zone at 30–35°C. They are strongly sensitive to acidity, with optimum at pH 7·0–8·0. A wide range of organic compounds may serve as carbonaceous food—fatty and oxy-acids, higher and lower alcohols, mono-, di-, and polysaccharides, etc. (Mockeridge, 1915; Gainey, 1928; Winogradsky, 1932). The actual fixation of nitrogen is brought about by a highly specialized system of enzymes, *azotase* (Burk, 1934), of which a specific component, *nitrogenase*, is capable of combining directly with elementary nitrogen. This enzyme-complex has so far, except for a still unconfirmed statement by Bach et al. (1934), resisted all attempts at isolation, and its production and activity appear inseparably linked with the synthesis of cell substance. Burk (1934) therefore describes it as "growthbound", and suggests the name *phyo-enzymes* for this type of enzymes. The nitrogenase requires a certain concentration of calcium (or strontium) for its functioning, is incapable of any activity at reactions below pH 6·0, and is strongly activated by even minute concentrations of molybdenum or to a lesser degree vanadium. The primary product of nitrogen fixation is not precisely known; that it should be ammonia, as supposed by Winogradsky (1932), is not definitely proved (Burk and Horner, 1936). According to Endres (1935) and Virtanen and Laine (1937), an oxime compound seems involved. Most of the fixed nitrogen is present in the cultures as cell material, and only small quantities of combined nitrogen (Endres, 1935; Roberg, 1935; Virtanen and Laine, 1937), or none at all (Meyerhof and Burk, 1928), are secreted into the medium as long as growth takes place. When the medium is exhausted of nutrients and growth has ceased, a rapid production of ammonia from the cell material sets in (Roberg, 1935; Burk and Horner, 1936).

Besides elementary nitrogen, *Azotobacter* can assimilate nitrate, ammonia, and simple amino compounds. All these compounds interfere in a remarkable way

[6] No attempt is made here to review the whole literature on *Azotobacter* and nitrogen-fixing bacteria in general. Reference may be made to de' Rossi (1932*c*), Waksman (1932), Burk (1934), and Russell (1937).

with the fixation of free nitrogen, apparently not merely by preferential assimilation, but by actual inactivation of the nitrogenase; Burk and Lineweaver (1930) observed this effect already at concentrations of 0·5 mgm. NO_3– or NH_4–N per 100 c.c. of medium. Bortels (1936) claims that with certain concentrations of molybdenum or vanadium (the action of which latter appeared to be supported by wolfram) nitrogen may still be fixed in the presence of higher concentrations of combined nitrogen. If this is generally valid, it will have an important bearing on our conceptions of the activity of *Azotobacter* under natural conditions.

Azotobacter transforms carbon compounds practically quantitatively into carbon dioxide, water, and cell substance. The amount of nitrogen fixed is generally close to 10 mgm. per gm. of sugar consumed, and other carbon compounds are utilized with an efficiency roughly proportional to their heats of combustion (Gainey, 1928). The efficiency of nitrogen fixation, however, varies with the type of organism as well as with experimental conditions, as we shall discuss in detail later.

Stapp and Bortels (1936) claim to have observed a remarkable influence of weather conditions on the growth of *Azotobacter* in pure culture; it remains uncertain whether this "weather-factor" also operates under natural soil conditions.

Numerous spore-forming and non-spore-forming bacteria, as well as actinomycetes, yeasts and filamentous fungi, have been claimed to fix small quantities of nitrogen, not always on good evidence. In some cases (Bondorff, 1918; Selim, 1931) the gains of nitrogen indeed seem too large to be explicable as analytical errors, but many other claims seem less convincing. For instance, Löhnis and Pillai (1905–08) reported nitrogen fixation in many bacteria, among which they include *Bact. radicicola*, which, according to more recent studies (M. Löhnis, 1930), has never been proved to fix nitrogen outside the host plant. The source of error which M. Löhnis pointed out (loss of nitrogen from the sterile control medium) might have been present in many other cases, and many of the claims of nitrogen fixation by aerobic bacteria other than *Azotobacter* may therefore be regarded with scepticism (cf. de' Rossi, 1932*c*). That actinomycetes and fungi (apart from the species of *Phoma* producing mycorrhiza in the Ericaceae) are unable to fix nitrogen in ordinary laboratory media can be regarded as fairly certain (Roberg, 1931; Waksman, 1932). Some organisms of these groups, as well as numerous bacteria, have been claimed by Emerson (1917), Carter and Greaves (1928), J. D. Greaves (1929–31) and Greaves and Greaves (1932) to fix nitrogen in sterile soil, although not in solution media. Greaves and Greaves (1932) make the significant remark that the aggregate effect of large numbers of such weakly nitrogen-fixing organisms may be much more important than that of a few highly effective forms like *Azotobacter*. These experiments, however, have one patent weakness in common: no allowance was made for the possible loss of nitrogen from the sterile control soil during incubation (Pfeiffer et al., 1906; Warmbold, 1908), which loss might not have taken place in the inoculated soil (cf. M. Löhnis, 1930). Still the possibility of such a non-specific nitrogen fixation must be regarded as existing, and deserves attention.

No attempts have been made to explain the mechanism of nitrogen fixation in these organisms; Winogradsky (1926–28) suggests the possibility of a rudimentary power of fixation due to the general catalytic properties of microbial protoplasm—which may indeed be quite significant if common to a large proportion of the total soil microflora.

Algae as primary agents of nitrogen fixation have been the subject of much controversy. Previous statements on nitrogen fixation by green algae have been fully disproved by Bristol and Page (1923), who still admit that their work does not actually prove the non-existence of nitrogen-fixing algae. More recently, Drewes (1928), Allison and Hoover (1935), Winter (1935), and De (1939), have shown beyond any doubt that certain blue-green algae are capable of fixing nitrogen. The mechanism of fixation is totally unknown.

2. *Anaerobic organisms.*—Nitrogen fixation was first definitely proved in *Clostridium pasteurianum* by Winogradsky (1895), and was later shown by Bredemann (1909*b*) to be a common property of the butyric acid bacilli. Some of these organisms are strict anaerobes, while others are less sensitive to oxygen (Pringsheim, 1906). Although more tolerant of acidity than *Azotobacter* (Dorner, 1924; Willis, 1934), they yet have a definite optimum at approximately neutral reaction (Dorner, 1924). In pure cultures generally 2 to 3 mgm. N are fixed per gm. of sugar fermented, although some strains may fix 5 to 6 mgm. (McCoy et al., 1928), or even more (Kostytchev, 1924). The mechanism of fixation is not well known, but is often explained as a direct reduction of elementary nitrogen to ammonia by nascent hydrogen.

A facultative anaerobe, *Bac. asterosporus*, was shown by Bredemann (1909*a*) to fix small amounts of nitrogen—1 to 3 mgm. per gm. of sugar fermented. It seems uncertain whether this faculty is also displayed under strictly aerobic conditions.

The observations of Clausen (1931) on an exceptionally vigorous nitrogen fixation by anaerobic cellulose-decomposing bacteria still remain to be confirmed.

Of all these organisms, *Azotobacter* is generally assumed to be the most important under field conditions, although some authors, e.g. Bonazzi (1924), have suggested that the clostridia may really be equally or more important by virtue of their wider distribution in soils (Bredemann, 1909*b*) and their greater resistance to acidity.

Earlier Investigations on Non-symbiotic Nitrogen Fixation in Field and Pot Experiments.

Soon after the fundamental experiments by Berthelot and the first isolation of the bacteria in question by Winogradsky and Beijerinck, attempts were made to assess the importance of this process in the nitrogen economy of the soil, partly on more theoretical grounds, and partly on the basis of observations from vegetation experiments.

Among the theoretical estimates, we may mention that of Remy (1909), who calculated that a soil containing 2% humus might annually fix 50 kgm. N per hectare, under the assumption that one-eighth of all the soil humus were annually transformed by *Azotobacter*. Löhnis (1909) estimated that a fixation of some 40 kgm. N per hectare per annum might be expected, *provided* the soil received an annual supply of 4000 kgm. organic matter per hectare, *and* that all this were utilized by bacteria capable of fixing 1 part of nitrogen per 100 parts of organic matter consumed. (As mentioned above, Löhnis reckoned with a large variety of soil microorganisms as nitrogen-fixers.) He pointed out, however, that this represents an upper limit, and that the actual gain might well drop to 10 kgm. or less. Alway and Pinckney (1909), in a similar way, arrived at a more conservative estimate of 8 lb. N per acre annually. Among recent authors, Winogradsky (1932) confines himself to the qualitative statement that "le rôle fertilisant des

Azotobacters, producteurs d'ammoniaque synthétique, ne saurait être mise en doute" (l.c., p. 299), whereas Bonazzi (1924) regarded the process as displayed only under conditions of nitrogen starvation, and de' Rossi (1932*b*–*c*) in Italy, Beck (1935) in South Australia, and Lochhead and Thexton (1936) in Canada, also take a sceptical view, all pointing out the low numbers by which *Azotobacter* is normally represented in the soil. Clearly all such speculations will carry little weight unless supported by direct evidence of the actual gain of nitrogen.

Many attempts have been made to estimate such gains under field conditions, either by simple observations on crop yields, by periodical nitrogen determinations in one and the same soil, or by comparing the nitrogen content of cultivated and uncultivated soils of similar character.

Kühn (1901), in Germany, believed that he found evidence of vigorous nitrogen fixation in soil under permanent rye cultivation, since the crop yields did not decrease during 30 years of cultivation without nitrogenous fertilizers. Pfeiffer (1904) criticized these conclusions severely and pointed out the difficulty of distinguishing between nitrogen recuperation and simple depletion of the soil's own store of nitrogen. The much older experiments on Broadbalk, Rothamsted, show, in a plot under permanent wheat cultivation without nitrogenous fertilizers, a close balance between (*a*) nitrogen removed in the crops and (*b*) nitrogen added by rain and seed, plus decrease in nitrogen content of the soil, which seems to have come to an equilibrium at about 0·1% N (Hall, 1905*b*; Russell, 1937). According to Hall (1905*b*), the plot also loses (or did at that time lose) about 10 lb. N per acre annually with the drainage water, which loss thus seems to be covered by nitrogen fixation. This fixation may in part be due to leguminous weeds, especially *Medicago lupulina*. Hall therefore considered it doubtful whether non-symbiotic nitrogen fixation assumed significant proportions in arable soils. But in soil that had been left undisturbed for 19 years and carried a heavy vegetation of grass and very few legumes, Hall (1905*a*) observed a gain of nitrogen corresponding to at least 25 lb. per acre per annum.

Besides these fundamental observations and theoretical estimates (whence probably the frequently encountered statement in text-books that "non-symbiotic nitrogen fixation may be expected to add from 15 to 40 lb. N per acre per annum to the soil"), most data have come from the United States and from India, in which latter country wheat cultivation without nitrogenous fertilizers is ancient practice.[7]

Alway (1909) found large decreases in nitrogen content of Nebraska soils under wheat cultivation for 9 to 30 years, in comparison with virgin soils. The same was observed in soils from Saskatchewan, Canada, by Alway and Trumbull (1910). Upon the whole it is common experience that cultivation of the rich prairie soils of Canada is accompanied by great losses of nitrogen (Russell, 1937).

Bradley and Fuller (1910) found no appreciable difference in nitrogen content of Oregon soils under wheat cultivation for 17 to 30 years, and adjacent uncultivated soils. They assumed that nitrogen fixation maintained a nitrogen balance in the soil.

Stewart (1910) and Greaves (1914), in Utah, arrived at similar results, and also offered the activity of *Azotobacter* as an explanation. In another paper Stewart and Hirst (1914) suggest the possibility of utilization of nutrients in

[7] All the data discussed here refer to soils not fertilized with nitrogen, unless otherwise stated.

the subsoil, due to deep root development under arid soil conditions, and deposition of organic matter from plant residues in the surface soil.

Swanson and Latshaw (1919), in Kansas, found that soils cultivated for up to 45 years had lost nitrogen in comparison with uncultivated soils, but the losses were smaller under arid than under humid conditions. (No figures were given for the crops.)

Gainey et al. (1929) analysed a large number of soils in Kansas with 12 years' interval and found a general tendency to loss of nitrogen, which loss appeared small or insignificant in soils with a low nitrogen content (0·08–0·12% N). This was especially noticeable under wheat or barley, continuous or alternating with fallow. The authors conclude that a balance of nitrogen tends to become established at about 0·1% N (cf. Hall, 1905*b*, and Russell, 1937), where the losses of nitrogen were supposed to be compensated by the activity of *Azotobacter*.

Jones and Yates (1924), in Oregon, and Metzger (1936), in Kansas, observed strong decreases in nitrogen content of soils under permanent cereal cultivation. Metzger calculated an average annual decrease in soil nitrogen of 0·64% under permanent wheat and 2·28% under permanent maize. The loss was greatest in the first years of the experiment, and an equilibrium also tended to establish itself here.

Holtz and Vandecaveye (1938), in Washington, in a permanent fertilizing experiment found large losses of nitrogen from N-fertilized plots after 13 years, but considerable gains (allowing for the nitrogen carried away in the crops) in a few cases (control plot and plot receiving 2700 lb. straw per annum under permanent wheat cultivation), which apparent gains they ascribe to the activity of *Azotobacter*. Under alternating wheat and fallow there was a general tendency to loss of nitrogen besides that removed in the crops.

All these observations apply to the more or less arid parts of North America. In the more humid regions (New York State), Lyon and Wilson (1928) and Lyon and Bizzell (1933–34) observed gains corresponding to 17 to 38 lb. N per acre annually in permanent plot experiments of 9 to 10 years' duration, either under permanent grass or in legume-free-rotations. The gain was highest where the grass was mown annually and allowed to remain on the ground (cf. Hall, 1905*a*).

Salter and Green (1933), in Ohio, calculated that soil under permanent oats or wheat for 30 years lost annually 1·5% of its total nitrogen, and under permanent maize even twice this amount.

Prince et al. (1938), in New Jersey, observed an increase in N-content from 0·097 to 0·116% in plots fertilized with P and K and abandoned to weed growth for 24 years. Part of this gain, which corresponds to a total of 380 lb. N per acre in 2 million lb. of surface soil, or an average of 16 lb. per acre per annum, seemed to be due to wild leguminous plants.

In India, Wilsdon and Ali (1922), Lander and Ali (1925), Annett et al. (1928), and Sahasrabuddhe et al. (1932–36) carried out shorter or longer series of periodical nitrogen determinations in soil. Marked fluctuations in the nitrogen content were observed by all these authors, and were interpreted as alternating gains (by non-symbiotic fixation) and losses (by denitrification or by leaching). Sreenivasan and Subramanyan (1934) found similar fluctuations, but did not ascribe them to biological causes.

In Nigeria, Diamond (1937) observed the same phenomenon within few days and even hours. He pointed out that no soil microorganisms yet known could have brought about such changes.

This view is not shared by Fehér et al. (1936–37)[8] in Hungary; the fluctuations in nitrogen content of soil reported here are so extraordinary (sometimes several hundred per cent. within a few months!) that it seems extremely hazardous to correlate them with the changes in the comparatively low numbers of soil micro-organisms in general and nitrogen-fixing bacteria (the nature of which was not closely specified) in particular. It seems obvious that if non-symbiotic nitrogen-fixing bacteria could accomplish such effects, all use of nitrogenous fertilizers would be purposeless.

Bortels (1937), in Germany, mentioned an increase in humus and nitrogen content of plots treated for 4 years with molybdenum and vanadium salts, and ascribed the effect to the stimulation of *Azotobacter* by these salts. No detailed figures were given.

Finally we may mention an observation by Kostytchev (1924) on a Crimean soil that had produced good crops of tobacco for 35 years without nitrogenous fertilizers, and similar observations by Loew (1927) on soils from Brazilian coffee plantations. Both authors stress the importance of *Azotobacter* under tropical soil conditions, but give no quantitative data.

In Australia, the only work of this kind so far published is due to Howell (1911), who compared the nitrogen content of 9 Victorian wheat soils, cultivated for 6 to 30 years, with that of corresponding virgin soils, and found in most cases evidence of a loss of nitrogen far in excess of the amount carried away with the crops. In soils with a low nitrogen content (about 0·1% N) there was some indication of a nitrogen equilibrium having become established.

The evidence from the field experiments and observations is thus conflicting and difficult to evaluate, owing to the many sources of error involved. Probably the most important among these is the sometimes surprisingly large variability in the composition of the soil, as shown by Pfeiffer and Blanck (1912) in Germany, Prince (1923) in New Jersey, and Sreenivasan and Subramanyan (1934) in India, besides others (cf. also Thiele, 1905). Further disturbing factors are the losses caused by leaching of nitrates from the soil (varying, of course, with the precipitation) and by wind or water erosion, as well as gains represented by nitrogen brought down by the rain or fixed by wild leguminous plants. Finally there is the analytical error in the actual nitrogen determination, which can sometimes be considerable (Pfeiffer et al., 1906). All these circumstances in connection with the fact that exhaustion of the nitrogen reserves of a normal soil is a very slow process (Russell and Richards, 1920) make it difficult to decide whether the tendency to establishment of a constant nitrogen level, so often observed, represents a real equilibrium between gains and losses of nitrogen, or whether it means that the rate of loss is getting continually slower. The only fact that seems to be definitely established is, that rich soils lose nitrogen at a faster rate than poorer ones. And even if a permanent nitrogen-equilibrium has been established in the soil, most of the field observations give us no information on the relative amounts of nitrogen gained from the rain, from non-symbiotic nitrogen fixation, and from wild-growing legumes. Observations by Howard (1906) suggest that the last factor may in India be of much more importance than is usually appreciated, and the same may be the case in other countries, including Australia (cf. Howell, 1911).

[8] "Die Regenerierung des Gesamtstickstoffgehalts des Bodens wird nach unserer Ansicht nur durch die Tätigkeit der stickstoffbindenden Bakterien ermöglicht" (Fehér and Frank, 1936).

In pot experiments, which may be taken in a wider sense to include experiments in cylinders or masonry frameworks, most of these sources of error are ruled out, particularly the soil variability, and many important studies on the nitrogen economy of the soil have been carried out in this way. The most important papers referring to non-symbiotic nitrogen fixation are the following:

Richter (1899) grew successive crops of oats and mustard, and found evidence of a certain gain of nitrogen, which became noticeable as the content of available soil nitrogen decreased.

Voorhees and Lipman (1905) found small gains of nitrogen (about 3% of the initial) in unmanured soil planted with oats, and larger but irregular gains, even up to 34%, in soil with farmyard manure and planted with millet.

In cylinder experiments on open field, Lipman and Brown (1908) found no positive evidence of nitrogen fixation. Lipman and Blair (1920), in similar experiments continued for 20 years, again found no indisputable gains of nitrogen in cylinders where no legumes were grown, although there was some evidence that the nitrogen content approached a constant level in unfertilized cylinders where the crop yields were very low.

Pfeiffer et al. (1909–10) carried out extensive pot experiments with sterilized or untreated soil, unplanted or planted with oats or mustard. In the first series (1909) no indisputable gains of nitrogen were found, but in the second series (1910) the gains were considerable, averaging 1·034 gm. N per 14 kgm. of soil, or about 5% of the total N-content. The authors emphasize that such large gains could not be expected under field conditions. (It seems highly desirable that such experiments should be repeated on soils of different character and under different climatic conditions.)

In a later series of experiments conducted for 12 years with soil in masonry frames, Pfeiffer (1921) observed no gains of nitrogen by non-symbiotic fixation.

Gerlach (1934) carried out similar experiments for 12 years, using an artificial soil consisting of sand, kaolin, and mineral nutrients. The crop yields gave no indication of nitrogen fixation in untreated soil not carrying legumes, whereas some nitrogen was gained in soil receiving periodical dressings of glucose. Unfortunately no nitrogen determinations were made on the soil medium itself.

Lemmermann et al. (1910) carried out pot experiments with mustard and found small but significant gains of nitrogen, which amounted to 1 to 4% of the total nitrogen content of the soil, but which were smaller than the quantities of nitrogen taken up by the plants.

Wright (1920) conducted pot experiments with different soils and crops for 1 to 3 years, and found evidence of loss rather than gain of nitrogen under fallow as well as under non-leguminous crops.

A kind of transition between field and pot experiments is represented by the lysimeter experiment at Rothamsted (Russell and Richards, 1920): a soil kept free from vegetation for 47 years showed no evidence of gains of nitrogen other than that brought down by the rain, or losses other than through leaching of nitrate.

A special category of experiments is represented by those cases where nitrogen fixation has been artificially stimulated by addition of sugar to the soil. That notable gains of nitrogen and corresponding increases in crop yield can be obtained in this way was first shown in pot experiments by Koch et al. (1907) and Remy (1909), and later by Hutchinson (1918) who also showed that similar results could be obtained under field conditions (cf. also Russell, 1937); such use of

molasses as an indirect nitrogenous fertilizer has in recent years attracted considerable attention (Dhar et al., 1936–37; Russell, 1937). Even in pot experiments, however, this effect of sugar is not constant (Pfeiffer et al., 1910), and the same applies to experiments where less readily assimilable organic materials have been added in order to stimulate fixation. Hutchinson (1918) thus found large gains of nitrogen in sand culture experiments with addition of hay dust and inoculation with a mixture of *Azotobacter* and putrefactive bacteria. Heinze (1926) reported increased yields of oats in pot experiments with additions of straw to the soil and inoculation with *Azotobacter* and various microbial preparations. A complete nitrogen-balance was not reported. Koch and Rippel (cit. after Waksman, 1932) found no gain in nitrogen in 10-year pot experiments with addition of filter paper or straw to the soil, although sugar gave positive results.

In connection herewith, we might mention some sand culture experiments by von Caron (1934), indicating gains of nitrogen by barley inoculated with certain bacteria not closely specified, and experiments by Truffaut and Bezssonoff (1925), who claimed to have grown maize to maturity in sterile sand medium inoculated with a mixture of nitrogen-fixing bacteria. None of these experiments appear well documented, and the results do not so far seem to have been corroborated by other investigators.[9]

The evidence from these experiments is thus conflicting, like that from the field observations. Although it is certain that nitrogen fixation can be induced by adding sugar, etc., to the growth medium, we are still left in doubt as to the amount of fixation that may take place under natural conditions where such high concentrations of easily assimilable nutrients are not present. Also, the construction of a complete and reliable balance-sheet of nitrogen is a difficult matter, and it is not always clear whether the difficulties involved in making reliable determinations of the nitrogen content of large quantities of soil have been overcome (cf. Pfeiffer et al., 1906–09).

In both field and pot experiments the work has been predominantly chemical, and only in few cases (Dhar and Seshacharyulu, 1936; Fehér et al., 1936–37) have observations on the abundance of nitrogen-fixing bacteria been combined with the chemical analyses.

We now arrive at the pure laboratory investigations on nitrogen fixation, which exist in an almost overwhelming number, and which, besides pure culture studies on the morphology, physiology and taxonomy of nitrogen-fixing microorganisms, chiefly deal with (1) the distribution and numbers of nitrogen-fixing bacteria in soils under natural conditions, and (2) estimation of the "nitrogen-fixing power" of soils under laboratory conditions. Many investigations in this second direction have in the past been carried out by means of the solution method first introduced by Remy; the principle of this method is to inoculate a selective liquid medium with a definite quantity of the soil to be examined, and to determine the amount of nitrogen fixed after an arbitrary period of incubation. Although the gain of nitrogen can be expressed in terms of organic nutrients (usually sugar or mannite) consumed, the method gives little information on what would happen in the soil itself. When all necessary mineral nutrients are supplied, the method shows little beyond the mere presence or absence of nitrogen-fixing bacteria in the soil; if nutrients are omitted and nitrogen-fixing bacteria

[9] As to the general aspects of the now chiefly historically interesting problem of inoculation with other than root-nodule bacteria, see Waksman (1932). Some recent work in this direction by Russian investigators is abstracted by Starkey (1938).

artificially added (the inoculation principle of Christensen, 1915), the method may give information on the soil's supply of available mineral nutrients, especially phosphate, and has come into some use for this purpose. As a method for studying the nitrogen-fixing capacity, it is, not least due to the trenchant criticism of Winogradsky (1925–26), more and more becoming replaced by the soil method, in which a certain quantity of soil, with or without addition of organic materials, nutrient salts, etc., is incubated for a certain length of time and the resulting change in nitrogen content determined by chemical analysis of the soil before and after incubation. This was the principle in the pioneer work by Berthelot (1888–90) and Schloesing (1888), and it was nearly 20 years before the method was again applied systematically by Schneider (1906), Warmbold (1906), Koch et al. (1907) and Remy (1909). This method has the advantage of coming closer to natural soil conditions than the solution method, and its most severe limitation is the difficulty of detecting changes smaller than one or two per cent. of the total nitrogen content of the soil.

A number of important contributions have been published by Winogradsky (1925–32), whose methods of "spontaneous cultures", however, aim chiefly at determining the nature and density of nitrogen-fixing bacteria present rather than the amount of fixation which they bring about in the soil itself. The method of determining the relative nitrogen-fixing power of soils on big plates of silicic acid gel with mannite (Winogradsky, 1926–28) really only differs from the solution method in being more strictly selective for *Azotobacter* and in giving quantitative expressions for the relative density of this organism.

Experimental.

All nitrogen-fixing microorganisms, with exception of the blue-green algae, require organic compounds as sources of energy; in Australian wheat soils, the chief groups of organic materials that might come into consideration, are the following:

i. The structureless organic matter of the soil ("humus"). According to the present state of our knowledge, this is largely unavailable to the nitrogen-fixing organisms.

ii. Straw, stubble and roots of cultivated plants (especially wheat and oats) and weeds.

iii. Organic compounds secreted by the roots of higher plants.

iv. Organic compounds elaborated by lower photosynthetic plants (algae).

If the nitrogen requirements of the wheat crops must be compensated by non-symbiotic nitrogen-fixation, we should expect nitrogen-fixing organisms to figure prominently in the transformation of the rather limited quantities of these materials and actually to derive their nitrogen from the atmosphere—or else autotrophic nitrogen-fixers (blue-green algae) must frequently find favourable conditions for active growth and nitrogen-fixation.

A fixation of merely 20 lb. nitrogen per acre annually would approximately meet the nitrogen requirement of the average wheat crop in New South Wales, and under conditions where such a gain could take place regularly, wheat cultivation could, so far as nitrogen is concerned, go on indefinitely. Since any attempt to detect the gain of such a quantity of nitrogen under field conditions would obviously be futile, the present work has been carried out purely under laboratory conditions. Firstly, a survey of the occurrence of *Azotobacter* and nitrogen-fixing clostridia in a number of Australian soils was made, and several representative strains of *Azotobacter* were tested in respect of their nitrogen-fixing capacity.

Secondly, nitrogen fixation in the soil itself was studied by incubating a number of typical wheat soils under varying conditions that should enable organic compounds of the groups mentioned above to become utilized by nitrogen-fixing organisms. The guiding principle in these experiments has been to correlate the changes in nitrogen content found by chemical analysis with the "biological reaction" (Winogradsky, 1925) resulting from the addition of organic compounds to the soil; particular attention was given to the question of the relation between cell counts of *Azotobacter* and quantity of nitrogen fixed. Finally, a series of investigations were made on the production of nitrate and ammonia from the organic ("humus") nitrogen in a number of soils, chiefly from the wheat belt.

(*a*). *Methods.*

Total nitrogen in soil was determined by the Kjeldahl method. At first (soils No. 1–15 in Table 2) the usual method of digestion with concentrated acid was used: finely ground air-dry soil was heated gently for 15–20 minutes with concentrated H_2SO_4 containing 4% salicylic acid to fix the nitrate; after reduction with sodium thiosulphate or zinc powder, potassium sulphate and copper sulphate were added, the mixture was heated until all dark colour had disappeared, and then boiled gently for another 3 hours. It was not until this time that the importance of using dilute sulphuric acid was realized (Bal, 1925; Sreenivasan, 1932). Subsequently a modification of the method of Olsen (1927) was used. Most of the soils to be analysed were very rich in ferric compounds, and it was therefore desirable to avoid the use of up to 5 gm. of reduced iron for reduction of the nitrate, as recommended by Olsen, since the very bulky precipitate resulting therefrom interferes badly with distillation. It was found that zinc powder could be used instead of iron for reduction of the comparatively small quantities of nitrate present in the soils examined here. A series of control analyses of KNO_3-solutions of known concentration showed that quantities of 0·98 to 1·40 mgm. NO_3–N could, with the procedure described below, be recovered with an accuracy of 95–100%, which is close to the titration error; larger amounts—2·80 mgm.—gave significant losses (about 15%). Also when added to nitrate-free soil, quantities of 1·25 mgm. NO_3–N (91·2 parts per million of soil) could be recovered with an accuracy of 95·3 $\pm$ 1·32%. Since the quantity of NO_3–N in the amount of soil used for each analysis never exceeded 0·8 mgm. (usually much less), the method may safely be regarded as satisfactory for the recovery of nitrate within the limits obtaining in the present experiments, although zinc-reduction is unsuitable in case of soils very rich in nitrate (cf. Olsen, 1927, and Sreenivasan, 1935).

The procedure of analysis was as follows: 4 to 20 gm. of soil, depending on its humus content, were placed in a 300 c.c. Kjeldahl flask, and 1 gm. of zinc powder, 5 gm. of K_2SO_4, 20–25 c.c. water and 20 c.c. conc. H_2SO_4 were added. After standing for a few minutes, with repeated shaking, the mixture was boiled slowly for 10–15 minutes, 0·5 gm. $CuSO_4$ was added (if this is added together with the zinc, there results a violent evolution of gas, accompanied by a loss of nitrogen, even with small concentrations of nitrate), and the heating was increased until the water had boiled away and the actual digestion started; if the soil is rich in organic matter, it is preferable not to add the potassium sulphate until the foaming is over. Heating was continued until all dark colour had gone, and then for 3 hours more, during which time the acid was kept slowly boiling (if this is not observed, too low results are obtained, as well as if the heating is

discontinued earlier). After cooling, the mixture was diluted with about 100 c.c. of distilled water and boiled for a few minutes in order to break up any cement-like material. The contents of the digestion flask were then by repeated washings (4–6 times) transferred to a distillation flask, leaving the sand behind in the Kjeldahl flask; a small excess of 20% NaOH was added, and ammonia was distilled off; 28/n H_2SO_4 and NaOH were used for the titration, with methyl red as an indicator. Before titration, the acid was boiled to expel the carbon dioxide and cooled under protection from the atmosphere A blank determination of nitrogen in the reagents was of course subtracted from the titration results. Usually 3 or 4 parallel determinations were made, 5 or 6 in cases of less satisfactory agreement. Extra determinations by this method were done on those soils that had previously been analysed by the "dry" digestion method; no significant differences were found, so that in these soils the "dry" digestion had given correct values (cf. Olsen, 1937). Yet the "wet" digestion is to be preferred, firstly because the digestion proceeds much more quickly, and a better agreement between the parallels is usually obtained (cf. Sreenivasan, 1932), and secondly because soils actually do exist in which the "dry" digestion gives too low results even if the heating is continued for 3 hours after clearing. This was the case with a heavy black basaltic loam (No. 17, Table 2), the type of soil which, according to Bal (1925), is most liable to give low results with dry digestion. The following percentages of nitrogen in dry soil were found:

By "dry" digestion:	By "wet" digestion:
(*a*) 0·1606%	(*a*) 0·1876%
(*b*) 0·1626%	(*b*) 0·1885%
(*c*) 0·1617%	(*c*) 0·1911%
Average: 0·1616%	0·1891%

The sediment was dark and coarsely granular after the dry, but light grey and finely divided after the wet digestion. Although Olsen (1937) found no difference by the two methods in the soils examined by him, there can be no doubt that the addition of water is a necessary precaution, as was also pointed out by Ashton (1936), owing to the ever-present possibility of encountering a soil like the one mentioned.

In some series of experiments, copper sulphate was replaced by 0·2 gm. of selenium, as recommended by Ashton (1936). This proved to be a most efficient catalyst which gave complete clearing of the mixture 20–30 minutes after the start of the actual digestion. Mercury was also tried, but was found to give no higher results than copper sulphate with wet digestion and heating for 3 hours after clearing; its use was therefore given up.

Trials were also made with the Davisson-Parsons method, in which the nitrate is first reduced with Devarda's alloy in alkaline solution (the method of Sreenivasan (1935) is a modification hereof). This method, besides being rather cumbersome, gave no higher results than the acid-reduction method, and was therefore abandoned.

Nitrogen determinations in sand or sand-kaolin mixtures were made as in soil, but on 20–40 gm. of material. These materials, as well as sandy soils, are best weighed off for analysis in a moist condition in order to avoid segregation (cf. Olsen, 1927).

Nitrogen in solution cultures of *Azotobacter* and other microorganisms was determined by the same method, but with only half the quantity of reagents.

A general survey of the agreement between the parallel determinations of nitrogen in soil is given in Figure 1. The coefficients of variability (standard deviation in per cent. of mean of parallel determinations) in 283 nitrogen determinations in soil are here arranged in groups of 0·25%. (The summary does not include the data in Table 8 from analyses with short digestion time, nor the analyses of sand and sand-kaolin mixtures.) The distribution of the frequencies around the mean (1·23%) is strikingly skew. There are cases of serious disagreement corresponding to a standard deviation of ± 4%, but these are quite exceptional; in no less than 194 cases (68·5% of total) we have a standard deviation less than ± 1·5%, which with only 3 parallel determinations corresponds to a mean error less than ± 0·87.

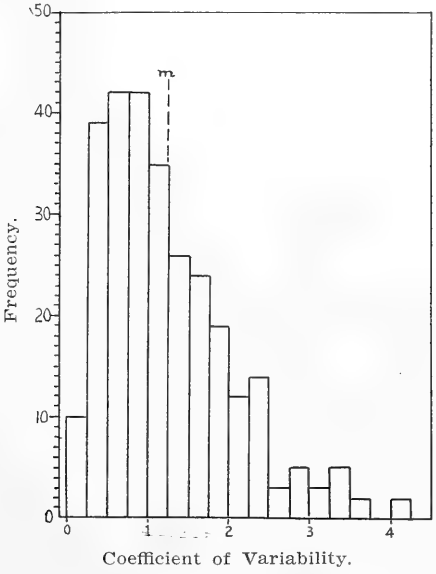

Fig. 1.—Distribution of coefficients of variability in 283 determinations of nitrogen in soil.

Nitrate in soil was determined in a water-extract obtained by leaching 25–75 gm. of air-dry soil with distilled water on a Buchner funnel. The extract was boiled slowly for 1–2 hours with NaOH and $KMnO_4$, the excess of permanganate reduced with a few drops of alcohol, and nitrate was determined by distillation with 1 gm. of Devarda's alloy.

Ammonia was determined by the method of Bengtsson: repeated extraction of a similar quantity of air-dry soil with 0·5 m. KCl, and distillation with MgO. Methyl red and 28/n H_2SO_4 and NaOH were used for the titrations.

(It has sometimes been stated—e.g. Richardson, 1938—that determinations of nitrate and ammonia in soil should be carried out without previous air-drying, which tends to increase the amounts. In view of the recent findings by Waksman and Madhok (1937) this increase might, however, seem to be apparent rather than real so far as nitrate is concerned, and nitrate was the chief form of inorganic soil nitrogen in the present experiments, where the amount of NH_4–N rarely

exceeded 6 parts per million of soil. No serious error need therefore be expected from the air-drying, which greatly facilitated the extraction.)

Determinations of nitrate and ammonia were carried out in duplicate, except in a few cases where there was only sufficient material for one determination. Before the actual determination, qualitative tests were made by extracting 5 gm. of soil with 5 c.c. 0·5 m. KCl and testing a few drops of the filtrate with diphenylamine-sulphuric acid for nitrate (including nitrite, for which no special test was made) and with Nessler's solution for ammonia. If no visible reaction was observed, the quantitative determination was omitted.

All figures for total, nitrate and ammonia nitrogen are in the subsequent tables expressed in terms of parts per million of soil dried to constant weight at 98° C. (abbr. "p.p.m.").

pH-determinations were made colorimetrically by the drop-ratio method of Gillespie on soil extracts obtained by centrifugation of a suspension of air-dry soil in distilled water in the ratio 1:2. Comparatively few soils were so acid as to come below the useful range of brom-cresol-purple (pH 5·5). In these cases it was possible to use methyl red which did not undergo any visible decolourization within the short time necessary to take the readings. Electrometric measurements by means of the quinhydrone electrode were tried, but gave in many instances obviously erroneous results, probably because of the presence of active manganese.

For *counts of Azotobacter* a silica-gel medium with mannite was first tried, as prescribed by Winogradsky (1925–26), but this was later abandoned in favour of an agar medium of the following composition: dextrine 10·0 gm.; K_2HPO_4 0·5 gm.; $MgSO_4$ 0·2 gm.; $FeCl_3$ 0·05 gm.; Na_2MoO_4 0·025 gm.; $CaCO_3$ 5·0 gm.; agar 20·0 gm.; H_2O 1000 c.c. This medium, while not giving such a luxuriant and uncontaminated growth of *Azotobacter* as the silica-gel medium, has the advantages of being less laborious to prepare, easy to sterilize, and of a much firmer texture. For counting purposes there seems to be little to choose between agar and silica-gel media, as found by Curie (1931), de' Rossi (1932*a*), and Turk (1936). Plates for counting were prepared by the method first introduced by Beijerinck (1921) and later used by de' Rossi (1932*a–b*): 4 to 15 gm. of soil were shaken for 3 minutes with sufficient sterile tap water to give a suspension of an initial dilution of 1:3 to 1:10 (higher dilutions were prepared for soils where the growth of *Azotobacter* had been stimulated by addition of organic matter), and portions of 0·2 or 0·4 c.c. of suspension were transferred to usually 3 or 5 parallel plates of sterile dextrine agar in ordinary 10 cm. Petri dishes. The inoculum was spread out as evenly as possible over the surface of agar by means of a stout L-shaped platinum wire, and the excess of water was allowed to evaporate before the dish was closed.[10] The plates were incubated at 28–30° C.; *Azotobacter*-colonies were usually counted after 5 days, but plates on which they did not appear were incubated for at least one week before being discarded; no colonies were ever seen to appear after still longer incubation. The identification of the *Azotobacter*-colonies was greatly facilitated by the circumstance that practically the only species encountered was *Az. chroococcum*, whose colonies on this medium were large, dense and easily distinguishable and showed the characteristic dark pigment after 3 to 4 days (cf. Omeliansky and Ssewerowa, 1911). Plate i, figures 1 and 2, show the appearance of two typical plates.

[10] This is necessary in order to avoid confluent growth of *Azotobacter*. Repeated tests with exposure of sterile plates to the laboratory air for 10-15 minutes showed no contamination with *Azotobacter*.

The reliability of the plate counts of *Azotobacter* was tested by calculating the index of dispersion (Fisher, 1930):

$$\chi^2 = \frac{S(x - \bar{x})^2}{\bar{x}},$$

where x represents the number of colonies per plate, $\bar{x}$ the mean, and $S(x - \bar{x})^2$ the sum of squares of deviations from the mean. If the colony counts give a reliable picture of the density of organisms in the suspension, the values of χ^2 should be distributed with a known frequency (Fisher, 1930, Table III) round a mean value equal to the number of parallel plates minus one. The result of this calculation on the first 100 3-plate counts and the first 70 5-plate counts (not including the many instances where only one or two *Azotobacter*-colonies were found on 3 or 5 parallel plates) is shown in Table 1.

TABLE 1.

Distribution of Values of χ^2 in Plate Counts of Azotobacter.

100 3-plate Sets. (n=2)			70 5-plate Sets. (n=4)		
χ^2	Frequency.		χ^2	Frequency.	
	Expected.	Observed.		Expected.	Observed.
0	1	3	0	0·7	1
0·0201	1	0	0·297	0·7	0
0·0404	3	2	0·429	2·1	1
0·103	5	5	0·711	3·5	3
0·211	10	9	1·064	7·0	8
0·446	10	13	1·649	7·0	5
0·713	20	12	2·195	14·0	11
1·386	20	20	3·357	14·0	17
2·408	10	8	4·878	7·0	12
3·219	10	13	5·989	7·0	6
4·605	5	9	7·779	3·5	1
5·991	3	3	9·488	2·1	4
7·824	1	1	11·668	0·7	1
9·210	1	2	13·277	0·7	0
	100	100		70	70

There is here in both sets a good agreement between observation and expectation. If anything, there is a tendency to excess among the higher values, but obviously excessive values of χ^2 were only found in one or two instances. The

method must therefore be regarded as satisfactory for determination of the number of *Azotobacter*-cells (or cell-aggregates) capable of developing into colonies on the agar medium.

The same medium was used for isolation and maintenance of pure cultures of *Azotobacter*.

Qualitative tests for presence of Azotobacter were made by inoculating 5 gm. of soil into 50 c.c. of sterile Beijerinck's mannite solution (2% mannite and 0·02% K_2HPO_4 in tap water) in 300 c.c. Erlenmeyer flasks, with addition of about 0·5 gm. $CaCO_3$. The flasks were incubated at 28–30°C. for at least one week and watched for appearance of the characteristic *Azotobacter*-pellicle. In cases of doubtful pellicle formation the surface scum was examined microscopically for presence of *Azotobacter* and a loopful of it streaked out on dextrine agar; this, however, was quite rare. The solution method seems in recent years to have come into disrepute, partly through the criticism of Winogradsky (1925–26), and the view has also before been expressed (e.g. Gainey, 1923) that a large number of *Azotobacter*-cells in the inoculum may be required in order to induce pellicle formation. Few attempts, however, have been made to compare the results of the solution method with those obtained by the methods introduced by Winogradsky. Düggeli (1924) and Wenzl (1934) made counts of *Azotobacter* both on agar plates and by dilution in mannite solution; they found that the solution method gave counts as high as, or even higher than, the plate method. Beck (1935) compared the silica-gel plate and the solution method (on 9 soils only) and found typical pellicles developing only from those soils that also showed *Azotobacter* on the plates.

In the present investigation there were 102 simultaneous plate counts and solution tests carried out. They showed the following agreement:

		Presence of *Azotobacter* by solution test.		
		Positive.	Negative.	Total.
Presence of *Azotobacter* by plate count.	Positive	30	5	35
	Negative	18	49	67
	Total	48	54	102

In 79 cases (77·4%) the two methods have shown agreement. In the remaining 23 cases, the solution method has shown presence of *Azotobacter* more than 3 times as frequently as the plate method. In all cases where the plate method gave a count of 10 or more *Azotobacter*-colonies per gm. of soil, a more or less typical pellicle developed in the mannite solution. In the 5 cases where the plate method gave positive and the solution method negative results, the plate counts indicated only 3–5 *Azotobacter*-colonies per gm. of soil. Unless very large plates inoculated with 1 to 2 gm. of soil be used, the solution method thus seems actually better adapted for detecting a sporadic presence of *Azotobacter*, and there is no reason to think that the results found by means of this method by earlier investigators (e.g. Christensen, 1915; Gainey, 1923) give a false picture of the distribution of *Azotobacter* in soil, as suspected by Winogradsky (1926). Yet it is desirable to combine it with other methods, not least in view of the discovery by Smith (1935) of *Azotobacter*-strains incapable of utilizing mannite.

Tests for presence of anaerobic nitrogen-fixing bacteria (butyric acid bacilli) were made in a modified Winogradsky's glucose solution, containing 10·0 gm. glucose, 0·5 gm. K_2HPO_4, 0·2 gm. $MgSO_4$, 0·2 gm. NaCl, 0·02 gm. $FeCl_3$, 0·01 gm. Na_2MoO_4, 10·0 gm. $CaCO_3$, and 1·0 gm. agar in 1000 c.c. H_2O. The medium was filled in ordinary test tubes to a height of 10 cm., sterilized, inoculated with soil

suspension corresponding to 0·1 gm. of soil, and incubated at 28–30°C. When gas formation appeared, the sediment was examined microscopically for presence of clostridia staining blue with Lugol's iodine solution. No attempt was made to count these organisms by cultural methods, in view of the extremely low percentage of the actual number of individuals that may be capable of reproduction in artificial media (Dorner, 1924).

Direct microscopic counts of total numbers of bacteria in soil were carried out by the indigo method of Thornton and Gray (1934). Rose bengale was used for staining instead of erythrosine. The counts were usually made in 50 microscopic fields from 10 drops of soil suspension of a dilution of 1:4 to 1:10. Separate counts were made of *Azotobacter*- and *Clostridium*-like organisms which, however, only rarely were so numerous that they could be counted with any reasonable accuracy (standard error less than ± 30%). The standard percentage error of the counts was estimated by the formula of Fisher:

$$\% \text{ S.E.} = 100\sqrt{\frac{1}{I} + \frac{1}{B}} \qquad \text{(Thornton and Gray, 1934)}$$

where I and B represent the total numbers counted of indigo particles and bacteria, respectively.

All numbers of microorganisms are expressed on the basis of soil dried at 98°C.

(*b*). *On the Occurrence of Nitrogen-fixing Bacteria in Australian Soils.*

A large amount of research has been done on the distribution of *Azotobacter* in soils from nearly all geographical regions (for references, see Waksman, 1932, and de' Rossi, 1932*c*). The earlier qualitative tests by means of the solution method have shown that the soil reaction is a factor of prime importance in controlling the distribution of *Azotobacter* in soil (Christensen, 1915). Further studies by Gainey (1923) and numerous later investigators have shown that a certain critical point exists at pH 6·0, above which occurrence of *Azotobacter* is common and below which it is rare. (The same pH-value, as shown by Burk, Lineweaver and Horner (1934), represents the limit of acidity for functioning of the nitrogen-fixing enzymic complex.) Yet the occurrence of *Azotobacter* in soils considerably more acid than pH 6·0 is by no means excluded (Gainey, 1923; Vandecaveye and Anderson, 1934, and others). Loew (1927) mentions a frequent occurrence of *Azotobacter* in tropical soils of acid reaction (pH not stated). Altson (1935) reported the isolation, from acid soil in Malaya, of a species of *Azotobacter* that seemed sensitive to $CaCO_3$ and capable of nitrogen fixation in media of pH 4·8–5·0; unfortunately the study of this remarkable organism was far from complete. A similar (identical?) organism has recently been described by Starkey and De (1939). Apart from certain observations by Jones and Murdoch (1919), Beijerinck (1921) and Düggeli (1924), few attempts were made to estimate the actual numbers of *Azotobacter* in soil, until Winogradsky (1925) introduced new methods, consisting partly in microscopic examination of the soil and partly in "spontaneous cultures" in selective media. On the basis of tests on silica-gel medium, Winogradsky (1926) distinguished three categories of soil in respect of nitrogen-fixing capacity: "active" soils, showing development of 2000–3000 *Azotobacter*-colonies per gm. of soil; "less active" soils, showing a variable but smaller number, and inactive soils, not showing development of *Azotobacter*. The maximal number of colonies reported by Winogradsky (1928) was 12,600 per gm. Similar tests on silicic-acid or agar media by other authors (Curie, 1931,

Vandecaveye and Anderson, 1934, and Turk, 1936, in U.S.A., Lochhead and Thexton, 1936, in Canada, Ziemecka, 1932, in England, de' Rossi, 1932*b*, in Italy, Wenzl, 1934, in Austria, De and Pain, 1936, in India) have given results in agreement herewith: like Jones and Murdoch (1919) and Beijerinck (1921), these authors found that the maximal numbers of *Azotobacter* rarely exceed a few thousand per gm. of soil and often reach only a few hundreds. It is common experience that nitrogenous fertilizers tend to reduce the numbers of *Azotobacter* (Düggeli, 1924; Winogradsky, 1928; Ziemecka, 1932; Lochhead and Thexton, 1936), but a rich *Azotobacter*-flora is usually assumed to be associated with generally high soil fertility (Remy, 1909; Beijerinck, 1921). Comparatively high numbers (up to 21,000 per gm.) were found by de' Rossi (1932*b*) who, unlike most other investigators, used soil suspension instead of the soil itself as an inoculum for the plates; some aggregates of *Azotobacter*-cells may hereby be broken up and the colony-count increased.[11] In agreement herewith, similar high numbers (15,000 or more per gm.) were reported by Düggeli (1924) and Burgess (1929), who used the method of dilution in liquid media. Besides these, some extraordinary numbers have now and again been reported. Dhar and Seshacharyulu (1936) found 1·3 to 2·8 mill. *Azotobacter* per gm. by plate counts in soil from plots *not* treated with molasses, and Kostytchev (1924) mentions a Crimean tobacco soil with more than 10 mill. *Azotobacter* per gm. In the first case it seems uncertain whether all the colonies counted were really *Azotobacter*, and in the second it is not stated whether cultural or microscopic methods were used. Several Russian investigators quoted by Dianowa and Woroschilowa (1931) claim to have found similar or even much higher numbers of *Azotobacter* by microscopic methods, but these findings, as Dianowa and Woroschilowa point out, are inconclusive, since other bacteria may produce cell types morphologically indistinguishable from *Azotobacter*.[12]

Anaerobic nitrogen-fixing bacteria of the butyric acid bacilli group are almost constant soil inhabitants, as first shown by Bredemann (1909*b*), and their numbers as indicated by cultural methods are generally higher than those of *Azotobacter* (de' Rossi, 1932*c*; Willis, 1934).

Few publications have yet appeared on the occurrence of nitrogen-fixing bacteria in Australian soils. Darnell-Smith (1912) reported the isolation of *Azotobacter* from three soils from New South Wales. Lewcock (1925) stated that he found *Azotobacter* constantly by the solution method in a not specified number of soils from South Australia, and thought that stimulation of their activity by phosphatic fertilizers was the cause of the general inefficiency of nitrogenous fertilizers. Beck (1935) arrived at entirely different results; by the use of silica-gel plates with mannite (sometimes combined with solution tests) he found *Azotobacter* in only 10 (all of pH 6·9 to 7·4) out of 33 South Australian soils; the maximal colony count was 560 per gm. It is to be noted that all the samples had been stored from 1 week to 8 months between sampling and testing. Penman and Rountree (1932), using the same technique, found *Azotobacter* in numbers of 50 to 260 per gm. in an approximately neutral Victorian soil under wheat or fallow, in which latter case it generally seemed more abundant. The authors concluded without any direct experimental evidence, that the vigorous nitrate production during fallowing was due to the combined action of *Azotobacter* and nitrifying bacteria. Swaby (1939) found *Azotobacter* present in 21 out of 80

[11] Swaby (1939), however, found only small increases in colony numbers, when soil suspension was used as an inoculum instead of the undisturbed soil.

[12] Winogradsky (1925) and Rossi et al. (1936) make the same reservation.

Victorian soils of pH 4·1–8·8, by plate counting on glucose agar. The highest number was 1600 per gm., and only 3 soils of pH 7·0–8·8 contained more than 100 per gm.; very few soils of pH 6·0 or less contained *Azotobacter* at all. *Clostridium butyricum* was found constantly in 57 soils, in numbers up to 1640 per gm., but mainly represented by spores.

The present investigations were carried out on 85 soil samples, mostly from the wheat district of New South Wales. A general description of the soils from which the samples were taken is found in Table 2. The geographical distribution of these soils is the following:

From New South Wales (65 samples):

Within the wheat belt (55 samples):

Northern Tableland and North-Western Slope: Nos. 16–18, 64–67, 80–82 (10 samples).

Central Tableland: Nos. 10, 11, 45–48, 57, 58, 72, 73 (10 samples).

Central Plain: Nos. 6, 7, 70, 71 (4 samples).

Central Western Slope: Nos. 53, 54, 74, 75, 78, 79 (6 samples).

South-Western Slope: Nos. 1, 2, 12–15, 19–21, 35, 38–42, 51, 52, 63, 76, 77 (20 samples).

Riverina: Nos. 49, 50, 83–85 (5 samples).

Outside the wheat belt (10 samples): Nos. 3–5, 8, 9, 44, 55, 56, 59, 60.

From Victoria (15 samples, all within the wheat belt): Nos. 22–30, 36, 37, 61, 62, 69, 70.

From Queensland (5 samples):

Within the wheat belt: Nos. 31–34.

Outside the wheat belt: No. 43.

The approximate location of the samples is shown on Text-figure 2.

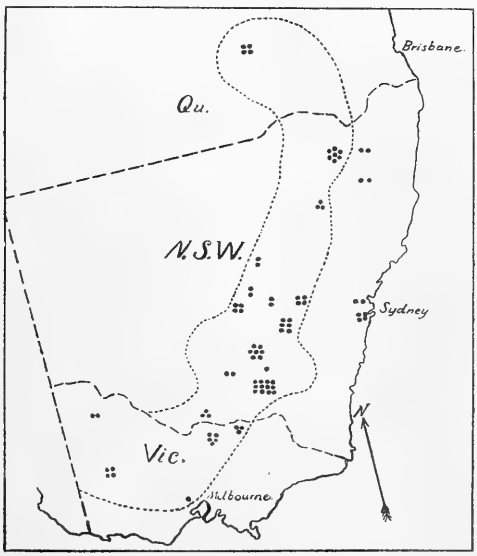

Fig. 2.—Map showing approximate location of soil samples (except No. 43, in Queensland). Broken lines: State boundaries. Dotted line: approximate boundaries of the wheat belt.

TABLE 2.

General Description of Soils Examined. Occurrence of N-fixing Bacteria.
(Soils marked * are from localities outside the wheat belt.)

Journal Number and General Character of Soil.	H_2O %.	pH.	*Azotobacter.* In Mannite† Solution.	*Azotobacter.* By Plate Count.	Clostridia in Glucose Solution.
1.—Red loam, good wheat field. Wagga, N.S.W. Sampled Nov., 1934, examined Jan., 1936 ..	(air-dry)	6·0	−		+
2.—Grey-brown loam, poorer wheat field. Same locality. Sampled Nov., 1934, examined Jan., 1936	(air-dry)	6·5	−		+
*3.—Coarse dark sand, uncultivated. Rose Bay North, Sydney. Sampled Feb., 1935, examined Jan., 1936	(air-dry)	4·8	−		
*4.—Heavy red loam, rich in humus. Lucerne field, northern tablelands, N.S.W. Sampled Dec., 1934, examined Jan., 1936	(air-dry)	5·5	−		
*5.—Heavy red loam, Same character and locality as No. 4. Sampled Dec., 1934, examined Jan., 1936	(air-dry)	4·7	−		
6.—Red loam, wheat stubble. Condobolin Exp. Farm, N.S.W. Receiving 156 lb. super. per annum. Sampled 18/1/36, examined 23/1/36..		5·6	−		
7.—Same soil type and locality as No. 6. Wheat stubble, unfertilized. Sampled 18/1/36, examined 23/1/36		5·1	−		
*8.—Grey sand mixed with clay, uncultivated. University of Sydney. Sampled and examined 11/2/36		7·4	+		
Do. after drying				9	
*9.—Black loam, rich in humus, under grass. University of Sydney. Sampled and examined					
(*a*) 7/3/36		6·9	+		
Do. after drying				590	
(*b*) 6/4/37	17·9	6·6	+	2360	
10.—Grey-brown sandy loam, wheat stubble. Cowra Exp. Farm, N.S.W. Receiving 168 lb. super. per annum. Sampled 16/3/36, examined 18/3/36		6·4	(+)		
Do. after drying			+	20	
11.—Same soil type and locality as No. 10. Wheat stubble, unfertilized. Sampled 16/3/36, examined 18/3/36		6·5	(+)		
Do. after drying			+	0	
12.—Yellowish-red loam, lucerne field (wheat until 1930). Wagga Exp. Farm, N.S.W. Receiving 112 lb. super. per annum. Sampled 30/3/36, examined 1/4/36		5·7	+		
Do. after drying			+	67	
13.—Same soil type and locality as No. 12. Unfertilized lucerne plot. Sampled 30/3/36, examined 1/4/36		6·1	−		
Do. after drying			+	0	
14.—Yellowish-red loam, fallow after oats. Temora Exp. Farm, N.S.W. Receiving 168 lb. super. per crop. Sampled 14/4/36, examined 17/4/36..		5·6	+		
Do. after drying			−	0	

† −, no pellicle ; +, pellicle formation ; (+), no real pellicle, but presence of *Azotobacter* revealed by microscopic examination.

15.—Same soil type and locality. Fallow, unfertilized. Sampled 14/4/36, examined 17/4/36		5·4	+	
Do. after drying			−	0
16.—Heavy brown loam, wheat field. Swan Vale, Inverell, N.S.W. Yield in 1935, 15 bus. Sampled 4/6/36, examined 8/6/36		7·1	(+)	
Do. after drying			(+)	0
17.—Heavy black loam, wheat field. Little Plain, Inverell, N.S.W. Yield in 1935, 36 bus. Sampled 3/6/36, examined 8/6/36		6·2	−	
Do. after drying				0
18.—Heavy red-brown loam, wheat field. Little Plain, Inverell, N.S.W. Yield in 1935, 37 bus. Sampled 3/6/36, examined 8/6/36		6·1	−	
Do. after drying			+	7
19.—Red sandy loam, wheat field. Junee, N.S.W. Cultivated 50 years. Av. yield, 26 bus. Sampled 8/6/36, examined 12/6/36		6·0	−	
20.—Red light loam, wheat field. Temora, N.S.W. Rotation wheat, fallow. Yield since 1929, 24–33 bus. Sampled 9/7/36, examined 14/7/36		6·0	−	0
21.—Red light loam, wheat field. Temora, N.S.W. Rotation wheat, oats, fallow. Yield of wheat since 1929, 18–35 bus. Sampled 9/7/36, examined 14/7/36		5·9	−	0
22.—Fine grey loam, fallow after wheat. Werribee Exp. Farm, Vic. Sampled 3/7/36, examined 6/7/36		5·8	−	
23.—Red-brown sand, wheat stubble. Mallee Research Station, Walpeup, Vic. Cleared 1933. Yield of wheat, 1934, 8·5 bus. Sampled 15/7/37, examined 17/7/37		7·6	+	0
24.—Red sand, poor in humus, wheat stubble. Same locality as No. 23. Yield of wheat in 1935, 27·5 bus. Sampled 15/7/36, examined 17/7/36		7·2	+	
25.—Yellowish-grey loam, wheat stubble. Rutherglen Exp. Farm, Vic. Cultivated 20 years. Fallow, wheat (or oats). Yield of wheat, 1935, 15 bus. Sampled 21/7/36, examined 23/7/36		6·5	+	
Do. after drying			−	0
26.—Heavy black loam, wheat stubble. Dookie Agr. College, Vic. Cultivated 50 years. Yield, 1935, 35 bus. Sampled 30/7/36, examined 4/8/36		7·5	−	
Do. after drying			(+)	7
27.—Fine red-grey loam, wheat stubble. Same locality. Cultivated 45 years. Yield 1935, 33 bus. Sampled 30/7/36, examined 4/8/36		5·8	−	
28.—Dark red loam, wheat stubble. Same locality. Cultivated 45 years. Yield 1935, 39 bus. Sampled 30/7/36, examined 4/8/36		5·7	−	
29.—Heavy grey loam, stubble pasture after wheat. Longerenong Agr. College, Vic. Cultivated 40 years. Wheat, stubble, pasture, fallow. Yield of wheat, 14–42 bus. Sampled 7/8/36, examined 25/8/36		7·6	(+)	0
30.—Same soil type and locality as No. 29. Under wheat crop. Cultivated 40 years. Same rotation and yield. Sampled 7/8/36, examined 25/8/36		7·7	(+)	
31.—Red-brown sand, poor in humus. Roma State Farm Reservation, Q. Vines and citrus fruit 20 years. Sampled 15/2/37, examined 25/2/37	(air-dry)	6·5	+	0

TABLE 2.—*Continued.*

Journal Number and General Character of Soil.	H_2O %.	pH.	*Azotobacter.* In Mannite† Solution.	*Azotobacter.* By Plate Count.	Clostridia in Glucose Solution.
32.—Red-brown sand, poor in humus, wheat stubble. Same locality as No. 31. Cultivated 20 years. Av. yield of wheat, 15·9 bus. Sampled 15/2/37, examined 25/2/37	(air-dry)	6·1	−	0	
33.—Red-brown sand, poor in humus, wheat stubble. Near localities No. 31 and 32. Sampled 15/2/37, examined 25/2/37	(air-dry)	6·2	+	0	
34.—Heavy black loam, pasture, cropped with wheat a few times last 8 years. Close to localities No. 31–33. Sampled 15/2/37, examined 25/2/37	(air-dry)	7·6	+	7	
35.—Red loam, wheat stubble. Wagga Exp. Farm, N.S.W. Sampled 28/4/37, examined 3/5/37	11·1	6·0	−	0	
36.—Yellowish-red loam, pasture. Rutherglen Exp. Farm, Vic. (wheat-oats-fallow until 1927). Sampled 29/4/39, examined 3/5/39	8·0	5·5	−	0	
37.—Yellowish-red loam, fallow after wheat. Same locality as No. 36. Yield of wheat 1936, 9 bus. Sampled 29/4/37, examined 3/5/37	4·5	5·6	−	0	
38.—Red loam, pasture. Wagga Exp. Farm, N.S.W. Sampled 26/5/37, examined 27/5/37	7·2	5·9	−	0	
39.—Yellowish-red loam. Same locality as No. 38. Lucerne field. Sampled 26/5/37, examined 27/5/37	6·6	5·7	−	0	
40.—Red loam, pasture. Same locality. Sampled 26/5/37, examined 27/5/37	6·6	6·5	−	0	
41.—Red loam, lucerne field. Same locality. Sampled 3/6/37, examined 9/6/37	11·8	5·9	−	0	+
42.—Red loam, stubble after wheat for hay in 1936. Same locality. Sampled 3/6/37, examined 9/6/37	13·0	6·0	−	0	+
*43.—Black loam, rich in humus, cotton field. Biloela, Q. Sampled 5/2/37, examined 5/4/37	6·6	7·3	+	740	
*44.—Heavy grey loam, experimental plots. School of Agriculture, Univ. of Sydney. Fallow; crop of field peas ploughed in on day of sampling. Sampled and examined 9/4/37	10·6	7·4	−	1640	+
45.—Red-brown sandy loam, under wheat. Bathurst Exp. Farm, N.S.W. (paddock No. 10). Sampled 13/8/37, examined 18/8/37	5·5	5·6	−	0	+
46.—Red-brown sandy loam, under wheat. Same locality as No. 45 (paddock No. 18). Sampled 13/8/37, examined 18/8/37	8·2	5·5	−	0	+
47.—Light brown sandy loam, under wheat. Cowra Exp. Farm, N.S.W. Cultivated 35 years. av. yield: wheat 25 bus., oats 36 bus. Sampled 19/8/37, examined 23/8/37	6·8	6·5	−	5	+
48.—Light brown sandy loam, under wheat. Same locality as No. 47. Cultivated 30 years. Yield similar to No. 47. Sampled 19/8/37, examined 23/8/37	8·0	6·3	+	11	+

† −, no pellicle; +, pellicle formation; (+), no real pellicle, but presence of *Azotobacter* revealed by microscopic examination.

49.—Red loam, fallow. Corobimilla via Narrandera, N.S.W. Cultivated 16 years, wheat, oats, fallow. Yield of wheat, 14–33 bus. Sampled 2/9/37, examined 6/9/37	9·6	5·8	—	6	+
50.—Red loam, fallow. Brobenah, N.S.W. Cultivated 35 years, wheat, oats, fallow, later wheat, fallow. Av. yield of wheat, 23 bus. Sampled 8/9/37, examined 10/9/37	9·0	6·1	—	6	+
51.—Red loam, under wheat. Temora Exp. Farm, N.S.W. Cultivated 8 years, wheat, fallow. Av. yield, 27 bus. Sampled 10/9/37, examined 14/9/37	10·9	6·6	—	0	+
52.—Another sample from the same field as No. 51. Sampled 10/9/37, examined 14/9/37	10·4	6·3	—	0	+
53.—Red loam, under wheat. Trangie Exp. Farm, N.S.W. Cultivated 20 years wheat, fallow, since 1929 wheat annually; yield 8–25 bus. Sampled 15/9/37, examined 16/9/37 ..	(air-dry)	6·7	—	0	+
54.—Another sample from the same field as No. 53. Sampled and examined same time	(air-dry)	6·8	—	0	+
*55.—Heavy brown loam, under wheat. New England Exp. Farm, N.S.W. Cultivated about 20 years. Sampled 23/9/37, examined 24/9/37..	12·5	5·7	—	0	+
*56.—Another sample from the same field as No. 55. Sampled and examined at the same time ..	12·7	5·7	—	0	+
57.—Light grey-brown sandy loam, under wheat. Bathurst Exp. Farm, N.S.W. Sample included wheat roots. Sampled 30/9/37, examined 1/10/37.					
Soil	4·5	5·5	—	0	+
Roots	17·0			0	
58.—Same soil type and locality as No. 57. Another field under wheat. Sample included wheat roots. Sampled 30/9/37, examined 2/10/37.					
Soil	4·9	5·5	—	0	+
Roots	20·0			0	
*59.—Fine grey sandy loam, under wheat for hay. Hawkesbury Agr. College, Richmond, N.S.W. Cultivated 40 years, cereals annually since 1930. Sample included wheat roots. Sampled 7/10/37, examined 8/10/37.					
Soil	(air-dry)	5·4	—	0	+
Roots				0	
*60.—Same soil type and locality as No. 59, under wheat for hay. Cultivated 35 years, cereals annually since 1924. Sample included wheat roots. Sampled 7/10/37, examined 8/10/37.					
Soil	(air-dry)	5·2	—	0	+
Roots				0	
61.—Heavy grey loam, under wheat crop. Longerenong Agr. College, Vic. Cultivated 40 years, mainly wheat, oats, fallow, since 1927. Yield of wheat, up to 53 bus. Sampled 5/10/37, examined 9/10/37	15·8	8·3	—	0	+
62.—Same soil type and locality as No. 61, under wheat crop. Cultivated 40 years, mainly wheat, pasture, fallow since 1927. Yield of wheat, 12–42 bus. Sampled 5/10/37, examined 9/10/37	16·5	8·3	—	0	+
63.—Yellowish-red loam, under wheat. Temora Exp. Farm, N.S.W. Since 1923, mainly wheat, fallow. Av. yield, 24 bus. Sample included wheat roots. Sampled 7/10/37, examined 11/10/37					
Soil	(air-dry)	5·7	+	0	+
Roots				0	

TABLE 2.—*Continued.*

Journal Number and General Character of Soil.	H_2O %.	pH.	*Azotobacter.*		Clostridia in Glucose Solution.
			In Mannite† Solution.	By Plate Count.	
64.—Heavy red-brown loam, rich in humus. Swan Vale, Inverell, N.S.W. Under wheat. Cultivated 20 years, wheat annually. Av. yield, 24–27 bus. Sampled 8/10/37, examined 11/10/37	13·9	6·4	−	0	
65.—Heavy black loam, under wheat. Auburn Vale, Inverell, N.S.W. Cultivated 15–20 years, lucerne 1929–35, also wheat annually. Yield never below 30 bus. Sampled 8/10/37, examined 11/10/37	15·6	6·7	−	0	+
66.—Heavy black loam, under wheat. Inverell, N.S.W. Cultivated 15 years, wheat, maize. Yield of wheat, 30–36 bus. Sampled 8/10/37, examined 11/10/37	20·4	6·5	+	6	+
67.—Heavy black loam, under wheat. Close to previous locality. Good yields after long fallow, otherwise poor. Yield of wheat, 15 bus. Sampled 8/10/37, examined 11/10/37	22·5	6·9	−	0	+
68.—Red loam, under wheat. Dookie Agr. College, Vic. Cultivated 50 years, since 1925 wheat, oats, fallow. Yield of wheat, 24–42 bus. Sample included wheat roots. Sampled 6/10/37, examined 12/10/37.					
Soil	9·0	5·7	−	0	+
Roots	17·0			0	
69.—Heavy dark-grey loam, under wheat. Dookie Agr. College, Vic. Cultivated 50 years, wheat, fallow since 1924. Yield 18–42 bus. Sampled 6/10/37, examined 12/10/37	17·7	7·0	−	0	+
70.—Red loam, under wheat. Condobolin Exp. Farm, N.S.W. Cleared 1930, oats 1931, since then wheat, fallow. Yield, 9–19 bus. Sampled 8/10/37, examined 13/10/37	(air-dry)	5·6	−	0	+
71.—Red loam, under wheat. Same locality as No. 70. Old cultivated paddock, since 1930 wheat, fallow. Yield, 7–13 bus. Sampled 8/10/37, examined 13/10/37	(air-dry)	5·7	−	0	+
72.—Coarse sandy yellowish-red loam, under wheat. Cowra Exp. Farm, N.S.W. Cultivated 35 years, wheat, oats, fallow. Av. yield wheat, 25 bus.; oats, 36 bus. Sampled 11/10/37, examined 14/10/37. Sample included wheat roots.					
Soil	5·3	5·8	−	0	+
Roots				0	
73.—Light sandy, red-brown loam, under wheat. Cowra Exp. Farm, N.S.W. Cultivated 40 years, wheat, oats, fallow. Yield similar to No. 72. Sample included wheat roots. Sampled 11/10/37, examined 14/10/37.					
Soil	8·7	6·5	−	0	+
Roots				0	
74.—Heavy greyish-brown loam (typical of the Myall Belt), fallow. Nelungoloo, Parkes, N.S.W. Cultivated, wheat 20 years. Av. yield, 23 bus. Sampled 19/11/37, examined 25/11/37	(air-dry)	7·1	−	0	+

† −, no pellicle; +, pellicle formation; (+), no real pellicle, but presence of *Azotobacter* revealed by microscopic examination.

75.—Red loam, under wheat. St. Evans, Parkes, N.S.W. Cultivated 35 years, wheat, fallow. Yield, 30–36 bus. Sampled 20/11/37, examined 25/11/37	7·5	6·0	—	0	+
76.—Yellowish-red loam, under wheat. Wagga Exp. Farm, N.S.W. Cultivated 15 years, fallow, wheat (hay). Sample included wheat roots. Sampled 10/12/37, examined 13/12/37.					
Soil	(air-	5·9	—	0	+
Roots	dry)			0	
77.—Same soil type and locality as No. 76. Same rotation, crop harvested for grain. Av. yield, 22 bus. Sample included wheat roots. Sampled 10/12/37, examined 13/12/37.					
Soil	(air-	5·7	—	0	+
Roots	dry)			0	
78.—Red loam, wheat field sown after fallow. Trundle, N.S.W. Cropped 40 years, wheat, fallow. Av. yield, 15 bus. Sampled 14/6/38, examined 17/6/38	(air-dry)	5·5	—	0	+
79.—Same soil type and locality as No. 78. Stubble after wheat, 1937. Cultivated 35 years, wheat, fallow. Av. yield, 20 bus. Sampled 14/6/38, examined 17/6/38	4·8	6·3	+	0	?
80.—Red-brown loam, wheat field. Curlewis, Gunnedah, N.S.W. Wheat 3 years, after grazing 10 years. Sampled 20/6/38, examined 22/6/38	10·4	6·9	+	0	?
81.—Heavy brown loam, rich in humus. Locality near No. 80. Stubble after wheat, 1937. Sampled 20/6/38, examined 22/6/38	20·7	8·0	+	960	+
82.—Heavy dark brown loam, rich in humus. wheat field. Locality near Nos. 80 and 81. Cultivated for 3 years. Sampled 4/8/38, examined 8/8/38	22·2	7·9	+	0	+
83.—Red loam, wheat field. Finley, N.S.W. Cultivated 20 years, wheat, oats, fallow. Av. yield of wheat, 15 bus. Sampled 1/9/38, examined 5/9/38	8·3	5·9	—	0	+
84.—Red loam, wheat field. Finley, N.S.W. Yield and rotation similar to No. 83. Sampled 1/9/38, examined 5/9/38	11·0	6·0	—	0	
85.—Red loam. Finley, N.S.W. Fallow. Yield and rotation similar to Nos. 83 and 84. Sampled 1/9/38, examined 5/9/38	9·6	6·6	—	0	—

Soils No. 1 to 5 had been stored for a considerable time in an air-dry condition before examination, and were used only for tentative experiments, the results of which are not strictly comparable with the rest. The other samples were taken straight from the fields, and represent the top 6 inches of soil. Owing to the wide distribution of the localities sampled, only few samples could be taken by myself, and strict aseptic precautions could not be taken in the sampling; however, sterilized tins were provided for the samples where possible. The tests were carried out as soon as possible after the arrival of the samples at the laboratory, usually on the same day; if this could not be done, the samples were stored in a refrigerator until examination. In most cases not more than 5 days elapsed between sampling and microbiological examination.[13] After the tests had been made, the soil was

[13] The longer delay in case of Nos. 29 and 30 was due to misunderstanding concerning the dispatch of the samples, and in case of Nos. 31-34 to the author's illness.

spread out in a thin layer on clean paper, air-dried, ground, sieved through a 20-mesh sieve, and stored for future use.

All soils were tested for *Azotobacter* by the solution method and, after the silica-gel medium had been abandoned, also by plate counts on dextrine agar (3 or 5 parallel plates, dilution 1:10 to 1:25). The tests were repeated on some of the soils after air-drying. Tests for anaerobic nitrogen-fixers were carried out in 45 soils only.

The results of the microbiological examinations are seen in Table 2. *Azotobacter* is of rather infrequent occurrence, being present in only 27, or 32%, of the 85 soils examined (the few soils that showed presence of *Azotobacter* only after air-drying, viz. Nos. 13, 18, and 26, are not considered positive owing to the possibility of contamination). If we consider only the freshly taken samples from the wheat belt (omitting Nos. 1–5, 8, 9, 43, 44, 55, 56, 59, and 60) we have 72 soils, of which 23, or 32%, contain *Azotobacter*. The occurrence of this organism in relation to soil reaction is shown in Figure 3. We find here 42 soils of pH 6·0 and less, of which 5, or 11·9%, contain *Azotobacter*; the most acid soil in which it was found was No. 15, of pH 5·4. Among the 43 soils of pH above 6·0 there are 22, or 50·1%, that contain *Azotobacter*, which seems to have its greatest relative frequency in the pH-interval 7·0 to 8·0. The corresponding figures for the 72 fresh samples from the wheat belt are 14·4% at pH 6·0 and less, and 47·4% above pH 6·0. The graph also shows that a reaction of pH 5·5 to 6·5 is by far the most common in the wheat soils examined here, although of course the prevailing soil reaction in the vast areas of the wheat belt cannot be judged on the basis of these few observations; no systematic work has yet been done on this question in New South Wales.

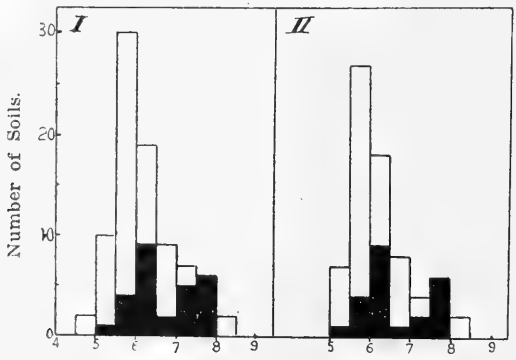

Fig. 3.—Occurrence of *Azotobacter* in relation to soil reaction: I, all samples; II, fresh samples from the wheat belt. (Black part of columns indicates number of samples containing *Azotobacter*.)

Table 2 further shows that *Azotobacter* is usually present in quite small numbers—from 5 to 20 colonies per gm. of soil, or so few that they cannot be detected by counting on the number of parallel plates used here. Only 4 soils (Nos. 9, 43, 44 and 81) are really rich in *Azotobacter*, with numbers of 600 to 2,360 per gm. of soil, and only one of these—No. 81—is a wheat soil. The soils are all of pH 6·6 to 8·0, and are considerably richer in humus than the average.

Finally, no direct correlation can be traced between the general productivity of the soils and the presence or absence of *Azotobacter*. For instance, they are absent or only sporadically present in the Wimmera soils from Victoria (Nos. 29, 30, 61 and 62), which are representatives of the most fertile type of wheat soils in Australia.

Unlike *Azotobacter*, the clostridia were almost constantly present, being found in all the 45 samples examined, with the exception of No. 85, and possibly also Nos. 79 and 80, where some fermentation took place, but where clostridia could not be seen with certainty on microscopic examination.

Generally speaking the results thus agree well with those found in other parts of the world, and also with those of Beck (1935), although in the present series *Azotobacter* is definitely more common in acid soils (Beck's failure to find *Azotobacter* in soils of pH below 6·9 may be due to the use of stored soil samples, since *Azotobacter* tends to die out on storage in acid soils). The agreement with Swaby's (1939) results is excellent.

No other organism than *Azotobacter* ever produced more than a trace of growth on the dextrine agar. Before the *Azotobacter*-colonies became distinguishable, which usually happened after 48 hours, the plates generally showed many small dewdrop-like colonies which soon coalesced into a thin, colourless, mucoid layer over the whole plate; this growth came to a standstill after 3 to 4 days, and was never so conspicuous as to suggest the presence of nitrogen-fixing bacteria (cf. Winogradsky, 1926). The medium thus appears very selective for *Azotobacter*, but this of course does not prove that no other aerobic nitrogen-fixing microorganisms exist in the soil.

In connection with this experimental series we shall mention some observations on the occurrence of *Azotobacter* in the rhizosphere of wheat. The rhizosphere is the zone immediately surrounding the plant roots; it contains a microbial population far more abundant than that of the soil itself, because in this zone there is an extra supply of organic matter represented by decaying root particles and in some cases probably also organic compounds secreted by living roots (see Waksman, 1932). Thom and Humfield (1932) made the important observation that the plant roots exert a kind of buffer effect on the soil, and create an approximately neutral reaction in the rhizosphere and, according to Starkey (1931), the concentration of nitrate is lower here than in the soil itself. All these circumstances together suggest that nitrogen-fixing bacteria, and *Azotobacter* in particular, might find a suitable habitat in the rhizosphere even if the conditions in the actual soil were unfavourable, and that the rhizosphere generally would offer better opportunities for nitrogen fixation; Kostytchev (1924) and Loew (1927) have, chiefly on theoretical grounds, ascribed a great importance to the activity of *Azotobacter* under these conditions and, as mentioned previously, Truffaut and Bezssonoff (1925) and von Caron (1934) claim to have grown maize and barley in sand culture inoculated with *Azotobacter* or other (allegedly) nitrogen-fixing bacteria, which under these conditions presumably could only utilize the organic root secretions and dead root parts. The direct experimental evidence, however, is less positive. Beijerinck (1909), Poschenrieder (1929–30) and Truffaut and Vladykov (1930) observed the common occurrence of *Azotobacter* in the neighbourhood of the roots of different plants (legumes, cruciferous plants, wheat), without giving any numerical data. Lyon and Wilson (1926) grew timothy aseptically in sterilized soil inoculated with *Azotobacter*, and found about twice as high numbers of this organism in planted as in

unplanted soil; the numbers, however, were always abnormally high (several millions per gm.) in comparison with normal soil. Starkey (1929) and Gräf (1930), using the solution method, found no definite evidence of more intensive nitrogen fixation or higher numbers of nitrogen-fixing bacteria in the rhizosphere of various plants, although the general micropopulation was immensely richer here than in the adjacent soil. Also in later experiments, where he used the contact slide method of Rossi and Cholodny for direct microscopical observation, Starkey (1938) found *Azotobacter*-like organisms only sparsely represented among the micropopulation in the rhizosphere of various plants at different stages of growth. Krasilnikov (1934) found the organic root secretions of wheat, produced in aseptic sand culture, altogether unsuitable as food material for *Azotobacter*, while the secretions of maize were of only inferior value; these results might not necessarily apply under natural soil conditions.

In the present series of investigations there were 10 cases (Nos. 57–60, 63, 68, 72, 73, 76, 77) where a considerable amount of roots of still-growing wheat plants was present in the sample. In these cases a separate count of *Azotobacter* was carried out on the root material (5 parallel plates, dil. 1:50). The results, as on the soils themselves, were always negative, as shown in Table 2. If *Azotobacter* thus occurs at all in the rhizosphere of wheat growing on otherwise *Azotobacter*-free soil, it must be quite sporadically.

Other counts of *Azotobacter* were carried out in the rhizosphere of wheat growing on a soil favourable for growth of *Azotobacter* (No. 44, Table 2). A plot of about 25 square feet, upon which wheat was grown for demonstration purposes, was selected. Samples were taken from the beginning of September to the beginning of December, 1937, i.e. from the heading to the ripening stage of the wheat, with an additional sample in January, 1938, when the plot was left under stubble. Owing to the layout of the plots, samples could not be taken at a distance of more than 6 inches from the plants, so that the data refer only to "soil adjacent to roots" and "roots with adhering soil", the latter representing the rhizosphere (Thom and Humfield, 1932). At each sampling one or two plants were dug up to a depth of about 5 inches by cutting out a block of soil around their roots. The soil and roots were immediately brought to the laboratory and separated as completely as possible by shaking of the roots; platings were then carried out on the soil as well as the root material, of which another portion was used for moisture determination. Besides counts of *Azotobacter* on dextrine agar, some counts of other microorganisms were also made on glucose-casein agar (glucose 2·0 gm.; casein dissolved in n/10 NaOH, 0·2 gm.; K_2HPO_4 0·5 gm.; $MgSO_4$ 0·2 gm.; $FeCl_3$ 0·01 gm.; agar 20·0 gm.; H_2O 1000 c.c.; pH 6·5–6·6). Colonies of bacteria and actinomycetes were counted on this medium after incubation for 8 days at 28–30°C.

The results are found in Table 3. The numbers of *Azotobacter* in the soil itself during the vegetation period are much higher than in any of the soils from the wheat area, on 11th November even reaching 10,000 per gm.; in the rhizosphere the numbers are generally somewhat (up to 3 times) higher, but this is not a rule without exception. The counts on glucose agar show that the *Azotobacter*-population accounts for only an insignificant fraction of the total numbers of living microorganisms, not even including fungi and those bacteria that do not develop on the agar medium. This is especially the case in the rhizosphere, where the bacterial numbers are generally 5 to 10 times as high as in the soil, while the numbers of *Azotobacter* are but slightly increased; it is also of interest to note that the total numbers of bacteria in the rhizosphere are of an order of

TABLE 3

Azotobacter *in Soil and Rhizosphere of Wheat Plants.*

Date of Sampling.	H_2O % in Soil.	*Azotobacter* per gm. Dry Matter.		Ratio R/S.	Other Microorganisms. Mill. per gm.			
					Soil.		Rhizosphere.	
		Soil.	Rhizosphere.		Bact.	Act.	Bact.	Act.
9/4/37 (fallow)	10·5	1,640	—	—	—	—	—	—
6/9/37	11·2	3,700	10,800	2·7	—	—	—	—
13/9/37	8·2	1,610	4,050	2·5	—	—	—	—
20/9/37	7·3	4,100	1,270	0·31	—	—	—	—
28/9/37	5·1	1,920	3,310	1·7	84	10	586	14
5/10/37 ..	10·2	1,270	1,570	1·2	143	7	1,360	14
12/10/37 ..	10·4	2,160	1,870	0·87	107	13	740	30
20/10/37 ..	9·0	2,620	8,350	3·2	79	20	934	34
28/10/37 ..	15·2	1,790	4,300	2·4	138	8	940	27
10/11/37 ..	16·7	10,500	3,190	0·30	142	10	906	15
18/11/37 ..	9·6	1,460	2,860	2·0	98	8	(lost)	
26/11/37 ..	7·5	2,170	1,820	0·84	108	9	497	27
8/12/37 ..	8·8	1,510	2,020	1·3	83	10	494	33
18/1/38 (stubble)	9·5	550	—	—	29	10	—	—

magnitude comparable with those found by Starkey (1929), Gräf (1930), and Thom and Humfield (1932). These phenomena indicate clearly that the organic root secretions and sloughed-off root tissues are chiefly utilized by microorganisms other than *Azotobacter* (even under soil conditions favourable for this organism), and thus hardly serve as energy material for nitrogen fixation to any significant extent—in agreement with the findings of Krasilnikov (1934). We shall revert to this subject later.

(*c*). *Nitrogen-fixing Capacity of* Azotobacter *Isolated from Australian Soils.*

Azotobacter is relatively sparsely represented in Australian wheat soils. Before proceeding to the problem of their function in the soil itself, the actual nitrogen-fixing capacity of these organisms in pure culture may be discussed. This question has been widely studied in the past.

Contrary to the view commonly expressed in most earlier investigations, viz., that the fixation of elementary nitrogen is a process that involves the consumption of large quantities of free energy which has to be derived from the oxidation of carbon compounds, Burk (1934; see also Meyerhof and Burk, 1928) has shown by thermodynamical calculations that the fixation process as such requires little energy, and if this were the only physiological function of *Azotobacter*, the oxidation of 1·5 gm. of glucose to carbon dioxide and water would suffice for the fixation of 1 gm. of nitrogen. Bach et al. (1934) claim to have observed enzymic fixation of up to 0·279 gm. nitrogen per gm. of glucose—a yield which begins to approach the theoretical limit calculated by Burk. These findings, however, have not been confirmed by Roberg (1936) and Lineweaver (1938), and the final products of fixation are exclusively, or nearly so, represented by bacterial protoplasm. Since the cells of *Azotobacter* contain at least 4 to 5 times as much carbon as nitrogen, the theoretical yield is reduced to 80–100 mgm. nitrogen per gm. glucose, and even this limit cannot actually be attained, because a considerable proportion of the carbonaceous food is used for cell respiration

and given off as carbon dioxide, and there is often, besides the synthesis of nitrogenous cell substance, a formation of considerable amounts of non-nitrogenous intercellular substance (polysaccharides). Consequently, the yield of fixed nitrogen is in pure cultures under favourable conditions usually reduced to some 10 to 15 mgm. per gm. of glucose or mannite consumed. Higher yields have occasionally been reported. Certain strains, according to Hunter (1923), Kostytchev (1924), and Krishna (1928*a*) may fix 18–23 mgm. nitrogen per gm. glucose. (If we assume with Burk and Meyerhof (1928) and Burk and Lineweaver (1930) that the cell dry matter contains 10% N and 50% C, this would correspond to a utilization of about 23–29% of the glucose-carbon for cell synthesis, and the rest for other physiological activities, largely respiration; Ranganathan and Norris (1927) and Krishna (1928*a*) found that 65–72% of the glucose-carbon consumed was liberated as carbon dioxide). Krainsky (1910) grew *Azotobacter* in mannite solution on sand, and reported a remarkably efficient nitrogen fixation at low moisture content—1 mgm. nitrogen per 11 mgm. carbon liberated as CO_2, corresponding to fixation of about 36 mgm. nitrogen per gm. mannite used for respiration. Unfortunately no parallel experiments were made, and only the mannite-carbon liberated as carbon dioxide was taken into account (actually there was 0·5 gm. mannite present in the medium in which 4·12 mgm. nitrogen were fixed, and residual mannite was not determined at the end of the experiment); Krainsky's method of calculation thus makes the yield appear unduly high, and the experiment cannot be accepted as valid proof of a particularly efficient nitrogen fixation in soil of low moisture content (cf. also Traaen, 1916). Koch and Seydel (1912), in a frequently quoted contribution, found a surprisingly economic utilization of the energy material in young agar cultures of *Azotobacter*, where after 2 to 3 days up to 70–80 mgm. nitrogen were fixed per gm. of glucose consumed; in older cultures the sugar consumption continued without being accompanied by a corresponding nitrogen fixation. The maximal gain is surprising, since it implies that the cells must have grown practically without respiring (actually, young cultures of *Azotobacter* respire most intensely (Meyerhof and Burk, 1928)), or else there must have been an accumulation of fixation-products of very much higher nitrogen content than the cell material. Later investigations by Hunter (1923), Cutler and Bal (1926), Ranganathan and Norris (1927) and Bortels (1936) have affirmed the general principle of decreasing efficiency in older cultures, but have shown far less extraordinary gains in young cultures (16–20 mgm. N per gm. of glucose).

In sharp contrast to most workers, who state that good aeration of the cultures makes for increased efficiency of the fixation process (Koch and Seydel, 1912; Hunter, 1923), Meyerhof and Burk (1928) found the ratio (c.c. N_2 fixed/c.c. O_2 consumed) *increasing* with decreasing oxygen tension and corresponding increase in the partial pressure of nitrogen; they concluded that an economical fixation of nitrogen might be expected in deeper soil layers with an atmosphere of low oxygen content.

It has frequently been claimed that low concentrations of sugar are utilized more economically by *Azotobacter* than higher ones (Waksman, 1932). Observations by Hunter (1923) and Krishna (1928*a*), however, have not confirmed this. Finally it may be mentioned that molybdenum deficiency reduces not only the rate of fixation, but also the yield per unit of sugar (Bortels, 1936).

To test the general efficiency of the forms of *Azotobacter* that commonly occur in Australian soils, 24 strains were isolated, most from the plate counts

and solution tests in Table 2, and some from incubation experiments with soils with various additions of organic materials. When plate counts were made from these experiments, a number of organisms other than *Azotobacter* were sometimes seen to produce quite a fair growth on the dextrine agar, particularly in high dilutions where the colonies were well separated. Some of these organisms (20 bacteria, 5 actinomycetes, 1 yeast, and 11 filamentous fungi) were isolated and tested qualitatively for growth in a nitrogen-free glucose solution where *Azotobacter* grew well. None of the bacteria produced more than a barely visible trace of growth after incubation for 5 to 9 weeks at 28–30°C., whereas the actinomycetes and particularly some of the fungi grew comparatively well. Some of those organisms that seemed to grow best were tested quantitatively together with the 24 pure cultures of *Azotobacter*; the experiments also included tests with an impure, but *Azotobacter*-free culture of blue-green algae, and an *Azotobacter*-free mixture of bacteria from the rhizosphere of wheat (from plate count 26/11/1937; inoculum was obtained by scraping off the thin bacterial growth between the *Azotobacter*-colonies). The organisms were grown in the following solution (modified from Bortels, 1936): Glucose 20·0 gm.; K_2HPO_4 1·0 gm.; $MgSO_4$ 0·5 gm.; $FeCl_3$ 0·1 gm.; Na_2MoO_4 0·05 gm.; $CaCO_3$ 5·0 gm.; H_2O 1000 c.c.

The medium was used in portions of 25 c.c. (= 0·5 gm. glucose) in 100 c.c. round flat-bottomed flasks, where it formed a layer about 12 mm. deep. The flasks were sterilized at 10 lb. pressure for 15 minutes and inoculated from young (2–3 days) slope cultures on dextrine agar. The organisms other than *Azotobacter* were tested after only a few transfers since isolation, and had never been grown on any nitrogenous medium in order not to risk a loss of what nitrogen-fixing power they might possess (cf. Selim, 1931). Four series of experiments were run; in the last two the medium was given an extra addition of 0·1% agar. As shown by Rippel (1937), this accelerates the growth which, particularly in the second series, was often rather slow (influence of a "weather-factor" as suggested by Stapp and Bortels (1936)?). Incubation took place at 28–30°C., usually 2 or 3 weeks for *Azotobacter*, and 3 to 5 weeks for the other organisms; very rapidly growing *Azotobacter*-cultures were analysed after 6–8 days, when the *chroococcum*-strains showed the beginning of black pigmentation around the edges of the surface of the solution. Before analysis, the cultures were diluted to 50 c.c. after careful distribution of the growth by shaking with glass beads, 2 c.c. were withdrawn and tested qualitatively for residual glucose with Fehling's solution, and the rest was analysed for total nitrogen. Control flasks were analysed immediately after inoculation, as well as after incubation, in which latter case they were inoculated immediately before analysis (the inoculum, however, was in all cases so small that a micro-method would have been necessary to detect its influence on the nitrogen content of the medium).

The results of these experiments are seen in Table 4. Not only did the control flasks absorb no nitrogen compounds from the atmosphere,[14] but even some of the small quantity of nitrogen present as impurities (chiefly of the calcium carbonate in series 1 to 3) seems actually to be lost during the incubation (cf. M. Löhnis, 1930). Therefore the *initial* nitrogen content of the controls has been subtracted from that of the cultures as correction for nitrogen in medium plus inoculum. With one or two exceptions in the first series, the *Azotobacter*-strains all grew well,

[14] The same was the case with control solutions of H_2SO_4 and NaOH placed in the incubator.

TABLE 4.

Nitrogen-fixing Capacity of Azotobacter *and Other Soil Microorganisms.*

Culture.	Incubation Days.	Total N in Culture. Mgm.	Gain of N. Mgm.	Glucose in Medium After Incubation.	N Fixed. Mgm. per gm. Glucose Consumed.	Remarks.
Ser. 1. Jan.–Feb., 1937.						
Control unincubated ..	0	0·20				
Control incubated (*a*)	15	0·14				
(*b*)	32	0·10				
(*c*)	32	0·02				
Az. chroococcum 8 (*a*)	14	6·56	6·36	Neg.	*12·7*	
(*b*)	14	6·23	6·03	Neg.	*12·1*	
25 (*a*)	14	7·63	7·43	Neg.	*14·9*	
(*b*)	14	7·51	7·31	Neg.	*14·6*	
10 (*a*)	14	7·34	7·14	Neg.	*14·3*	
(*b*)	14	6·42	6·22	Neg.	*12·4*	
11 (*a*)	14	7·26	7·06	Neg.	*14·1*	
(*b*)	14	6·27	6·07	Neg.	*12·1*	
12 (*a*)	14	4·43	4·23	Faint.	*>8·4*	
(*b*)	14	5·37	5·17	Pos.	*>10·3*	
16 (*a*)	14	1·88	1·68	Pos.	*>3·3*	(*a*): Scant growth.
(*b*)	14	9·33	9·13	Neg.	*18·3*	
30 (*a*)	21	1·14	0·94	Pos.	*>1·9*	Very scant growth.
(*b*)	21	1·21	1·01	Pos.	*>2·0*	
Fusarium sp. 14 ..	32	0·25	(0·05)		(Nil)	Scant growth.
Bacterium sp. 11 (*a*) ..	21	0·11	(Nil)			Growth hardly visible.
(*b*) ..	21	0·14	(Nil)			
Ser. 2. May–June, 1937.						
Control unincubated (*a*)	0	0·15				
(*b*)	0	0·17				
Control incubated (*a*)	21	0·07				
(*b*)	21	0·04				
Az. chroococcum sand-kaolin mixture plus straw (Table 15) (*a*)	14	4·29	4·13	Faint.	*>8·3*	
(*b*)	14	4·83	4·67	(Trace)	*>9·3*	
Az. chroococcum 34 (*a*)	14	4·55	4·39	Pos.	*>8·8*	
(*b*)	14	7·51	7·35	Neg.	*14·7*	
43 (*a*)	14	7·21	7·05	Neg.	*14·1*	
(*b*)	14	6·62	6·46	Neg.	*12·9*	

* 5 c.c. conc. acid added immediately after inoculation.

Az. chroococcum 44 (*a*)	14	7·06	6·90	Neg.	*13·8*	
(*b*)	14	5·71	5·55	Neg.	*11·1*	
31 (*a*)	21	4·95	4·79	Neg.	*9·6*	Slow growth.
(*b*)	21	5·06	4·90	Neg.	*9·8*	
33 (*a*)	21	5·43	5·27	Neg.	*10·5*	Slow growth.
(*b*)	21	5·42	5·26	Neg.	*10·5*	
32 (*a*)	21	5·62	5·46	Neg.	*10·9*	Slow growth.
(*b*)	21	5·13	4·97	Neg.	*9·9*	
Az. beijerinckii(?), sand-kaolin mixture plus straw (*a*)	21	5·42	5·26	Neg.	*10·5*	Slow growth.
(*b*)	21	4·72	4·56	Neg.	*9·1*	
Bacillus sp., sand-kaolin mixture plus straw (*a*)	30	0·11	(Nil)			No visible growth.
(*b*)	30	0·09	(Nil)			
Actinomyces sp., sand-kaolin mixture plus straw (*a*)	21	0·06	(Nil)			Scant granular growth.
(*b*)	21	0·09	(Nil)			
Dematium pullulans (?) 23 (*a*)	21	0·10	(Nil)			Very scant growth.
(*b*)	21	0·08	(Nil)			
Dark green unidentified fungus 30 (*Helminthosporium* ?) (*a*) ..	24	0·13	(Nil)			Scant flaky mycelium.
(*b*) ..	24	0·08	(Nil)			
Crude culture of blue-green algae (cf. Table 27) (*a*)	28	0·10	(Nil)			Trace of growth only.
(*b*)	28	0·06	(Nil)			

Ser. 3. Nov.–Dec., 1937. 0·1% agar added to glucose solution.

Control unincubated (*a*)	0	0·17				
(*b*)	0	0·11				
Control incubated (*a*)	21	0·12				
(*b*)	21	0·11				
Control incubated + H_2SO_4*	20	0·06				
Az. chroococcum 49 (*a*)	8	5·69	5·55	Neg.	*11·1*	Very rapid growth.
(*b*)	8	6·31	6·17	Neg.	*12·3*	
48 (*a*)	12	6·07	5·93	Neg.	*11·9*	
(*b*)	12	5·89	5·75	Neg.	*11·5*	
66 (*a*)	18	4·84	4·70	(Trace)	*>9·4*	(*a*): slow growth.
(*b*)	14	7·37	7·23	Neg.	*14·5*	
63 (*a*)	18	5·88	5·74	Neg.	*11·5*	
(*b*)	18	6·44	6·30	Neg.	*12·6*	
30 (*a*)	12	5·49	5·35	Neg.	*10·7*	Normal
(cf. Ser. 1). (*b*)	12	5·46	5·32	Neg.	*10·6*	growth.

TABLE 4.—*Continued.*

Culture.	Incubation Days.	Total N in Culture. Mgm.	Gain of N. Mgm.	Glucose in Medium After Incubation.	N Fixed. Mgm. per gm. Glucose Consumed.	Remarks.
Az. vinelandii	8	8·50	8·36	Neg.	*16·7*	Rapid growth.
Az.-free bacterial mixture from rhizosphere of wheat (*a*) ..	21	0·26	(0·12)	Pos.	?	Slight gas formation.
(*b*) ..	21	0·34	(0·20)	Pos.	?	
Ser. 4. July, 1938. 0·1% agar added to glucose solution.						
Control unincubated (*a*)	0	0·08				
(*b*)	0	0·06				
Control incubated ..	14	0·05				
Az. vinelandii (*a*) ..	6	6·92	6·85	Neg.	*13·7*	Very rapid growth.
(*b*) ..	6	6·43	6·36	Neg.	*12·7*	
Az. chroococcum 79 (*a*)	6	5·60	5·53	Neg.	*11·1*	Very rapid growth.
(*b*)	6	6·42	6·35	Neg.	*12·7*	
80 (*a*)	12	6·01	5·94	Neg.	*11·9*	
(*b*)	12	6·06	5·99	Neg.	*12·0*	
81 (*a*)	14	5·22	5·15	Neg.	*10·3*	
(*b*)	14	4·98	4·91	Neg.	*9·8*	
Az. chroococcum from mixed soil No. 31 + 33 + wheat straw (Table 19) (*a*) ..	12	6·11	6·04	Neg.	*12·1*	
(*b*) ..	12	6·05	5·98	Neg.	*12·0*	
Yellow mucoid bacterium from synthetic soil + water-extracted wheatstraw (Table 22)	21	0·01	(Nil)			Trace of growth only.
White bacterium from synthetic soil + untreated wheat straw (Table 22)	21	0·02	(Nil)			Growth not visible.

in most cases consuming all the glucose within 2–3 weeks and fixing 9 to 18 mgm. N per gm. glucose consumed. Where some glucose is left, the amount of fixed nitrogen generally corresponds to about 8 mgm. per gm. of glucose supplied. Duplicate cultures show a good agreement, with only few exceptions (strain 16, ser. 1; strain 34, ser. 2; strain 66, ser. 3). Strain No. 30, which almost failed to grow in the first series, showed normal growth and fixation on re-trial in solution with agar; it may be that this strain is particularly sensitive either to the accelerating influence of colloids (Rippel, 1937) or to a possible weather-factor (Stapp and Bortels, 1936).

The other organisms failed entirely to fix nitrogen under the conditions of the experiment, with the possible exception of the bacterial mixture from the wheat rhizosphere; there is here a mere trace of nitrogen fixation, accompanied by a slight gas formation; possibly some spores of clostridia had been lying dormant on the plates and had become introduced with the inoculum. The fungi, and particularly the one from soil No. 30 (a *Helminthosporium*?), produced a quite appreciable growth, but this is obviously due merely to ability to utilize the nitrogenous impurities of the medium, and not to nitrogen-fixing capacity.

An additional set of experiments was carried out to test whether the present *Azotobacter*-strains would fix nitrogen with particular efficiency in quite young cultures. In order to make conditions as favourable as possible, a very dilute glucose solution was used. In the first series it contained half the concentration of soluble salts of that of the previous experiments, in addition to 0·125% glucose, 0·1% agar, and 0·1% $CaCO_3$; portions of 80 c.c. (= 0·1 gm. glucose) were placed in wide flat-bottomed flasks, where the liquid formed a layer about 5 mm. deep. In the second series the basal solution was of the normal composition, with 0·2% glucose; 75 c.c. portions were used in round flasks of 1 litre capacity. Two normally growing strains of *Az. chroococcum* were tested in the first series, *Az. vinelandii* and a rapidly growing *Az. chroococcum* in the second. Controls were analysed immediately after inoculation only; in the first series an extra flask with sugar-free medium was included in order to see if the agar contained any available energy material; this was not found to be the case. After incubation for 48–96 hours at 28–30°C., the cultures were diluted to 100 c.c., of which 10 c.c. were tested for glucose and the rest analysed for nitrogen. The results are found in Table 5.

TABLE 5.

Nitrogen Fixation by Azotobacter *in Solution with Low Concentration of Glucose.*

Culture.	Incubation Hours.	Total N in Culture. Mgm.	Gain of N. Mgm.	Glucose in Medium After Incubation.	N Fixed. Mgm. per gm. Glucose Consumed.
Ser. 1. July, 1937. 80 c.c. 0·125% glucose-solution in flat-bottomed flasks.					
Control solution (*a*) ..	0	0·07			
(*b*) ..	0	0·09			
Az. chroococcum 44 (*a*) ..	48	1·22	1·14	Neg.	*11·4*
(*b*) ..	48	1·17	1·09	Neg.	*10·9*
34 (*a*) ..	48	0·87	0·79	Neg.	*7·9*
(*b*) ..	48	0·95	0·87	Neg.	*8·7*
Az. chroococcum— glucose-free solution ..	48	0·10	(Nil)		
Ser. 2. July, 1938. 75 c.c. 0·2% glucose solution in large round flasks.					
Control solution (*a*) ..	0	0·07			
(*b*) ..	0	0·09			
(*a*)	48	1·55	1·47	(Trace)	(*10·3*)
Az. vinelandii (*b*) ..	72	1·74	1·66	Neg.	*11·1*
(*c*)	96	1·76	1·68	Neg.	*11·2*
Az. chroococcum 79 (*a*) ..	48	1·47	1·39	Neg.	*9·3*
(*b*) ..	72	1·68	1·60	Neg.	*10·7*

There is absolutely no indication of any increased efficiency of nitrogen fixation in these experiments, although the conditions should here be in every respect optimal: short incubation time and low concentration of glucose to avoid accumulation of metabolic products in the medium, presence of a colloid, and a fully sufficient concentration of molybdenum (Bortels, 1936). In fact, strains 34 in the first series and *Az. vinelandii* in the second seem to fix less nitrogen per gm. glucose here than in the 2% solution with longer incubation. Koch and Seydel's (1912) observations are thus certainly not generally valid. There is a good reason to suspect that the lower efficiency in older cultures, as well as the less economical utilization of higher concentrations of sugar or mannite sometimes reported, may really have been caused by molybdenum deficiency of the medium; it is noteworthy that all these findings have been reported prior to the discovery of the function of molybdenum in nitrogen fixation by Bortels in 1930.

As a whole the experiments show that the *Azotobacter* generally occurring in Australian soils have a perfectly normal nitrogen-fixing capacity, and do not differ greatly from each other. The occasionally appearing *Az. beijerinckii* and *vinelandii* do not differ much in this respect from the common *Az. chroococcum*. The importance of these organisms in the nitrogen economy of the soil will thus presumably depend less upon strain-specificity than upon the quantity of energy material which they actually consume.

(*d*). *Nitrogen Fixation in Soils under Laboratory Conditions.*

The foregoing results, viz., that *Azotobacter* is usually either absent or only sparsely represented in the wheat soils, that the commonly occurring strains have no extraordinary nitrogen-fixing power, and that no other aerobic nitrogen-fixing microorganisms appear to be present, might seem to speak strongly against non-symbiotic nitrogen fixation as a factor of significance. Before drawing any final conclusions, however, we must turn to the method of nitrogen fixation experiments in the soil itself. Firstly, colony counts of *Azotobacter* may be counts of cell aggregates rather than of individual cells, and we know little about the relation between these counts and the actual fixation of nitrogen. Further, organisms of the butyric acid bacilli group may be capable of acting in the soil even at moderate degrees of moisture (Winogradsky, 1925), and finally we must not overlook the possible existence of organisms capable of fixing nitrogen when growing in the soil but not in the ordinary artificial media. In soils incubated under favourable conditions of moisture and temperature and with addition of such organic materials as might come into consideration as energy materials under natural conditions, all such organisms, both known and unknown, should be expected to find chances for displaying their activities. Several series of experiments have been undertaken from this point of view.

1. *Soils without Addition of Organic Matter.*

In looking for organic compounds that might serve as food substance for nitrogen-fixing bacteria, one would naturally first think of the organic matter normally present in the soil, either as still incompletely decomposed plant residues or as structureless "humus". Numerous attempts have been made to prove that a measurable fixation of nitrogen may take place on the basis of these materials. The first of these were the fundamental researches by Berthelot (1888–90), who in his first investigations on soils very poor in organic matter found increases of up to 40% of the nitrogen content after several months, but

later with more normal soils found more moderate gains of 5–15%. Nitrogen determinations were usually carried out only in duplicate by means of the now abandoned soda-lime method, occasionally controlled by the Dumas method. Most experiments were made on soil exposed to daylight, under laboratory, greenhouse or field conditions. Practically all subsequent investigators have used the Kjeldahl method in its various modifications for the nitrogen determinations. The following authors have reported gains of nitrogen in soils incubated under laboratory conditions without addition of organic matter:

Schneider (1906), in Germany, incubated soil from 15 differently fertilized plots for 6 weeks at room temperature and found gains of nitrogen in all cases—from 52 to 251 p.p.m., or 6 to 33% of the original nitrogen content. The analytical method was not described in detail.

Warmbold (1906), in Germany, reported small but irregular gains of nitrogen under similar conditions, even in sterilized soil. These statements were vigorously contested by Pfeiffer et al. (1906), and in later experiments Warmbold (1908) found definite losses of nitrogen by incubation of sterilized soil.

Koch et al. (1907), in Germany, found no significant increase in nitrogen content of soil incubated for up to 4 months at room temperature, but sometimes large gains (120–130 p.p.m.) after 8–10 months; the analytical error was clearly stated. The authors regard it as uncertain whether the effect was due to absorption of ammonia from the atmosphere or to other causes.

Krainsky (1908), in Russia, reported fixation of up to 130 p.p.m. nitrogen in soil kept for 3 months at room temperature. The gain was highest at low moisture content, where it was calculated that one part of nitrogen had been fixed for every 9 parts of carbon liberated as CO_2. Only two parallel determinations of nitrogen were made, and the method was not described in detail.

Remy (1909), in Germany, found gains of nitrogen, clearly exceeding the analytical error, in soils incubated 25 to 70 days at room temperature. The largest absolute gain (91·5 p.p.m., or about 10% of the original nitrogen content) was found in loam with addition of $CaCO_3$, but the largest relative gain (38·4 p.p.m., or 25% of the original) in $CaCO_3$-treated sand soil poor in humus and apparently devoid of *Azotobacter*. The gains were sometimes followed by losses. Some factor other than biological fixation seems to have been operating, as certain gains of nitrogen were sometimes observed where mercury chloride had been added to the soil (cf. de' Rossi, 1932*c*).

Lemmermann and Wichers (1914), in Germany, observed a gain of nitrogen (63·4 p.p.m., or about 16% of the original content) in a soil which served as control in a denitrification experiment. In several other series no significant changes were observed. The authors do not discuss these findings further.

Mockeridge (1917), in England, found gains of 110 to 200 p.p.m. nitrogen in two soils incubated for two weeks at room temperature. The soils were rich in nitrogen, and the gains represent only 4 to 6% of the original content. The differences appear significant, but the procedure of analysis was not described in detail. With addition of "bacterised peat" even larger gains were reported.

Zoond (1926), in England, reported similar gains (300 p.p.m., or about 8%) in a humus-rich soil incubated for 4 weeks at 25°C. with addition of 1% $CaCO_3$.

de' Rossi (1932*c*), in Italy, mentioned briefly an experiment suggesting nitrogen fixation by physico-chemical agencies in soil after heating or with addition of $HgCl_2$. Very small samples of soil (10 gm.) were used, and it is not clearly stated whether they were all analysed in a dry or moist condition.

Fehér (1933), in Hungary, worked on an initially strongly acid soil, which was sterilized, re-infected, and incubated for 13 months at different temperature, with and without restoration of the moisture content. At 15°C. large gains of nitrogen were found: in moist soil 60 p.p.m., or 13%, and in dry soil 106 p.p.m., or 24% of the initial content. At higher temperatures there was a tendency to loss of nitrogen (very marked at 55°C.). The method and error of analysis were not mentioned.

Sackett (1912) and Headden (1911–21), in Colorado, observed large gains of nitrogen in soils kept for 4 to 7 weeks at 28–30°C. Sackett found the strongest fixation at low degrees of moisture. Headden reported gains simultaneously with strong nitrate production, and stated that the gains could rise to 610 p.p.m., or nearly 50% of the initial content. Later, Headden (1922) observed gains of nitrogen in almost pure sand, corresponding to 10 times the initial content. He ascribed both the nitrogen fixation and the nitrification to the activity of *Azotobacter*. None of the authors describe the procedure of analysis in detail.

Greaves (1914), in Utah, incubated 16 soils for 6 weeks at 30°C., and reported gains of up to 168 p.p.m. nitrogen. In another contribution Greaves (1916) reported gains of 49 to 168 p.p.m. nitrogen in 3 soils incubated for 18 days at 30°C. One of these soils had continued to give good yields of wheat without nitrogenous fertilizers for 23 years, although it was poor in humus. Later again, Greaves and Nelson (1923) reported gains of 36 to 55 p.p.m. nitrogen in a calcareous soil incubated for 3 to 6 weeks at 28°C.; longer periods of incubation gave irregular results. (In all these experiments it appears that the gain of nitrogen was calculated as difference between nitrogen contents of untreated and sterile—presumably autoclaved—soil incubated under the same conditions.) In experiments with larger quantities of the same soil kept for 437 days at room temperature, Greaves and Nelson also found large but rather irregular gains, after 244 days even 160 p.p.m., or nearly 11% of the initial nitrogen content. The authors comment that "this soil in little less than one year had gained at the rate of 480 pounds of nitrogen per acre-foot of soil". The analytical error was not stated.

Fulmer (1917), in Wisconsin, gave figures suggesting a gain of 100 to 170 p.p.m. of nitrogen, or 4 to 6% of the initial, in field soil incubated for 6 weeks at 25°C., but stated cautiously that this might be due to the error of analysis.

Neller (1920), in New Jersey, mentioned briefly a gain of 7·7 to 9·4 mgm. nitrogen (in 200 gm. of soil?) in 4 soils from a fertilizing experiment. No further comments were made.

Murray (1921), in Washington, carried out nitrogen fixation experiments with straw; in the control soils he reported gains corresponding to about 17% of the original nitrogen content, which gains, in another experiment with addition of ammonium sulphate, even rose to 40%. Apparently only two parallel determinations were made, and the procedure of analysis was not described.

Lipman and Teakle (1925), in California, reported gains corresponding to 10–12% of the initial nitrogen content in both sterilized and unsterilized soil inoculated with *Azotobacter*. The differences are clearly significant, but it is not definitely stated whether sterilized or untreated soil served as control, nor was the analytical method clearly described.

Vandecaveye and Villanueva (1934) and Vandecaveye and Allen (1935), in Washington, incubated wheat soils for 115 to 165 days at room temperature and found large gains of nitrogen, sometimes exceeding 10% of the initial content

and accompanied by very small losses of carbon. Counts of *Azotobacter* and determinations of nitrate were also carried out. The authors remark (1935) that the gains could not be attributed to *Azotobacter*, which only occurred in comparatively low numbers. The analytical error was not stated.

Turk (1936), in Michigan, found gains of 80 to 222 p.p.m. nitrogen in 4 out of 6 wheat soils incubated for 12 weeks. One of the soils had pH 5·0 and contained no *Azotobacter*. The actual nitrogen contents of the soils, as well as the method of analysis, were not stated.

Walton (1915), in Punjab, reported a gain of about 6% of the original nitrogen content of a soil incubated for 3 weeks at 30°C. No further details were given.

Wilsdon and Ali (1922), in Punjab, found gains of up to 45% of the initial nitrogen content of soils in a series of experiments under conditions that were not closely defined. They concluded that the season was a factor of prime importance, and that soils tended to fix nitrogen, especially after long periods of drought.

Lander and Ali (1925) followed up these experiments and determined nitrogen in soils kept for up to 5 months at 30 to 35°C. In some cases they observed large gains of nitrogen, even increases from 0·0470 to 0·0823% N within one month; in other cases similar losses were found. These phenomena were interpreted as alternating nitrogen fixation and denitrification, although no bacteriological investigations were made. In spite of the irregularity of the results, the authors conclude that "Nature has provided a certain degree of remedy for the losses of nitrogen which take place during the removal of crops". The analytical method was not described in detail.

Sahasrabuddhe and Daji (1925) and Sahasrabuddhe and Ghatikar (1931), in Bombay, found similar results with soils incubated 2 or 4 weeks at 20 to 40°C.; gains of nitrogen were even observed in soil that had been heated to 100°C. (cf. de' Rossi, 1932*c*) and in soil containing as much as 62 p.p.m. of NO_3–N. Here, again, the method of analysis was not described in detail. Sahasrabuddhe and co-workers, as well as the previous Indian investigators, stress the importance of root and stubble remains of the crops as energy material for nitrogen fixation, without, however, carrying out any biological experiments.

De and Pain (1936), in Bengal, incubated 6 rice soils for 2 months at 33°C.; 4 soils showed gains corresponding to 40 to 120 lb. nitrogen per acre (the actual analytical data were not given). The highest gain was reported in a soil of pH 5·1 and not containing *Azotobacter*, which in the other soils occurred in numbers up to 2700 per gm. The authors think that this indicates the existence of still unknown but highly efficient nitrogen-fixing soil microorganisms.

Records of negative findings under similar conditions are comparatively few, but upon the whole better documented. Schloesing *père* (1888), in France, found no significant increases in nitrogen content of various soils after storage for 1–2 years; these experiments are interesting because of the systematic use of direct gasometric methods. Thiele (1905), in Germany, found similar results in sterilized soil inoculated with *Azotobacter* and incubated at 30°C., as well as in unsterilized soil stored in flasks under field conditions. In numerous experiments where the method of analysis was described in detail and the analytical error definitely stated, Lemmermann and Blanck (1908), Lemmermann, Blanck and Staub (1910), Lemmermann and Themlitz (1934), in Germany, and Christensen (1927), in Denmark, found generally no significant gains of nitrogen

in soils incubated without addition of energy material; occasionally there was indeed also in these experiments a small but apparently significant increase in nitrogen content; none of the authors, however, have explicitly ascribed this phenomenon to nitrogen fixation. (In the analytical data of Lemmermann et al. (1910) one notices a remarkably high content of NO_3– and NH_4–N, which could hardly be conducive to fixation.) de' Rossi (1932*d*), in Italy, found no gain of nitrogen in two soils incubated without addition of mannite for 10–12 days at 32°C., in spite of an appreciable multiplication of *Azotobacter*. In India, Meggitt (1923) found no gain of nitrogen in a soil which fixed large amounts on addition of sugar, and Bal (1928) observed only small and occasional gains which he did not consider significant.

Even if the extraordinary gains reported by Indian investigators may be fictitious, as pointed out by Bal (1925–28), the bulk of the evidence still seems to suggest that an intensive nitrogen fixation may, especially in soils from hot and dry climates like India and the western United States, take place at the expense of the organic matter normally present in the soil. If this is the case, the comparatively small amounts of organic matter must obviously be utilized much more economically than in pure cultures, whether by *Azotobacter* or by other organisms possibly capable of nitrogen fixation. It will appear from the survey given above, that the reported gains of nitrogen have largely been of the order of 5 to 10% of the original nitrogen content, or even higher; this is well beyond what we may expect to be able to detect analytically, and, if really existing, it would fully meet the nitrogen requirements of the crops. Experiments were therefore carried out in order to ascertain whether such processes take place in Australian wheat soils.

Thirty-three of the soils in Table 2 were used for this purpose. Portions of 120 to 180 gm. of air-dried, finely ground and sieved soil were moistened with distilled water to approximately 60% of their water-holding capacity,[15] placed in big Petri dishes (13·5 × 2 cm.), and incubated at 28–30°C. for 30 days, during which time the moisture content was restored every 2 to 3 days by addition of distilled water. Before and after incubation total nitrogen was determined (as well as ammonia and nitrate, which will be discussed later); in most cases counts of *Azotobacter* were also made. The experiments were carried out in duplicate, except with soils No. 1 and 2, the experiments on which were of a more tentative character. Only one dish with soil No. 9 was analysed, since this soil was abnormally rich in humus and was only included for the sake of comparison. Two soils, Nos. 6 and 7, were also analysed after 60 days, the second analysis being carried out on a mixture of equal parts of soil from the two parallels in the first period of incubation. Soil No. 8, which was of alkaline reaction, poor in humus and containing *Azotobacter*, was used in other experiments with addition of organic matter as a control soil designed to show optimal conditions for nitrogen fixation; it was therefore given an addition of 0·2% $CaHPO_4$. Soils No. 14 and 15 were exceptionally rich in nitrate at the outset of the experiment, which was therefore repeated: after incubation for 30 days, the soil which had been extracted with water for determination of nitrate was air-dried, re-moistened, and incubated

[15] It is difficult to get reliable estimates of the water-holding capacity, which may serve for comparison of light sand soils and very heavy clay soils, both of which types were represented in this investigation. It was therefore deemed preferable to rely on a subjective estimation of about 60% saturation by adding the water very slowly in small portions, until the soil had attained a fine crumbly texture without any stickiness.

for another period of 30 days, equal parts of soil from the two parallel dishes in the first period being used. Soil No. 35 deserves particular mention. Unlike the other samples, it was not taken to the depth of 6 inches, but represents the soil adhering to the roots of dead wheat plants (left without stubble-burning from harvest 1936 until the end of March 1937) to a depth of 2–3 inches, and was deliberately taken in such a way as to include a large proportion of dead root-material; an extra experiment was carried out on this soil with addition of 0·5% $CaCO_3$ and 0·025% Na_2HPO_4; this, together with the presence of large amounts of partially undecomposed plant material, should give particularly favourable conditions for nitrogen fixation. Soil No. 44 is somewhat comparable with this; it was not the same sample as in Table 2, but represents the soil adhering to the roots of wheat plants in the heading stage (13/9/1937, Table 3), and contained a certain amount of fine rootlets.

TABLE 6.

Numbers of Azotobacter *in Soils During Incubation at 28–30° C.*

(s+) and (s−) denote presence and absence, respectively, of *Azotobacter* in mannite solution.

Soil No. and pH.	Incubation Days.	*Azotobacter* per gm.	Soil No. and pH.	Incubation Days.	*Azotobacter* per gm.
31 (pH 6·5)	0 30	0 (s+) 13 (s+)	35 (pH 6·0)	0 30	0 (s−) 0 (s+)
32 (pH 6·1)	0 30	0 (s−) 5 (s−)	(35+$CaCO_3$)	30	(*a*) 66,500 (*b*) 54,300
24 (pH 7·4)	0 30	(s+) 0	34 (pH 7·6)	0 30	7 (s+) 18 (s+)
8 (pH 7·4)	0 30	9 (*a*) 5,900 (*b*) 4,400	15 (pH 5·4)	0 30	0 (s−) 0 (s−)
19 (pH 6·0)	0 30	(s−) 3 (s−)	23 (pH 7·6)	0 30	0 (s+) 0 (s+)
12 (pH 5·7)	0 30	67 (s+) 0 (s−)	51+52 (pH 6·4)	0 30	0 (s−) 0
25 (pH 6·5)	0 30	0 (s+) 0 (s+)	29 (pH 7·6)	0 28	0 (s+) 0 (s+)
21 (pH 5·9)	0 7 30	0 (s−) 0 0 (s−)	30 (pH 7·7)	0 30	(s+) 0
11 (pH 6·5)	0 30	0 (s+) 220 (s+)	26 (pH 7·5)	0 30	7 (s+) 140 (s+)
10 (pH 6·4)	0 30	20 (s+) 8 (s+)	16 (pH 7·1)	0 30	0 (s+) 640 (s+)
13 (pH 6·1)	0 30	0 (s+) 0 (s+)	44 (pH 7·4)	0 15 30	2,040 (s+) 2,190 2,340
20 (pH 6·0)	0 30	0 (s−) 0 (s+)	9 (pH 6·9)	0 30	590 (s+) 210 (s+)
14 (pH 5·6)	0 30	3 (s−) 0 (s−)			

The results of the *Azotobacter*-counts are shown in Table 6. A really striking increase in *Azotobacter* has taken place only in soil No. 8, to which $CaHPO_4$ had been added, and in No. 35 with addition of lime and phosphate. Otherwise we find only small increases, as in Nos. 11, 16, and 26, or none that can be considered significant at all. In the cases where *Azotobacter* were originally present in soil of pH less than 6·0 (Nos. 12 and 14) they appear to have died out during incubation, as might be expected (cf. Christensen, 1915; Gainey, 1923; Vandecaveye and Anderson, 1934); special acid-resistant forms thus do not seem to occur in these soils. Upon the whole the results agree with those of other investigators (de' Rossi, 1932*d*; Vandecaveye et al., 1934–35) in showing that the numbers of *Azotobacter* do not generally rise to a much different order of magnitude during incubation under favourable conditions of moisture and temperature, even in soils of neutral to alkaline reaction.

Table 7 shows the results of the nitrogen determinations. The significance of the difference in nitrogen content of soil before and after incubation was tested by applying the *t*-test of Fisher (1930, p. 107) for the comparison of two means. For this test we calculate the following statistics:

(1) Mean of determinations of nitrogen,

$$\bar{x} = \frac{S(x)}{n+1},$$

where $n + 1$ represents the number of parallel determinations, and $S(x)$ the sum of individual determinations.

(2) Variance resulting from pooling the sums of squares of deviations from the two means,

$$s^2\left(\frac{1}{n_1+1} + \frac{1}{n_2+1}\right) = \frac{(n_1+n_2+2)\left(S(x_1-\bar{x}_1)^2 + S(x_2-\bar{x}_2)^2\right)}{(n_1+1)\ (n_2+1)\ (n_1+n_2)}$$

and hence the standard deviation

$$s = \sqrt{\frac{S(x_1-\bar{x}_1)^2 + S(x_2-\bar{x}_2)^2}{n_1+n_2}},$$

(3) and $$t = \frac{\bar{x}_2-\bar{x}_1}{s}\sqrt{\frac{(n_1+1)\ (n_2+1)}{n_1+n_2+2}};$$

(4) $n = n_1 + n_2$,

where the indices *1* and *2* denote the two sets of estimations to be compared. From Fisher's Table iv the probability, P, of the difference being significant was found; if the value of P is less than 0·05 the difference may be regarded as significant. The data given in Table 7 are: the mean of the nitrogen determinations ($\bar{x}$), the number of parallel determinations ($n + 1$), sum of squares of deviations from the mean, ($S(x-\bar{x})^2$), apparent change in nitrogen content as difference between means of determinations before and after incubation ($\bar{x}_2-\bar{x}_1$), values of *t* calculated from these data, and the corresponding values of P. The pH values are also given, and in the final column the apparent change in nitrogen content as percentage of initial total nitrogen content ($100(\bar{x}_2-\bar{x}_1)/\bar{x}_1$), where $\bar{x}_1$ and $\bar{x}_2$ represent the means before and after incubation. In the table the soils are arranged in order of increasing nitrogen content.

TABLE 7.

Changes in Nitrogen Content of Soils Incubated 30 d. 28–30° C. without Addition of Organic Matter.

Soil No.	pH.	Total N, p.p.m., Mean. ($\bar{x}$).	n+1.	S $(x-\bar{x})^2$	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	Gain or Loss of N in % of Total Initial N.
31	6·5	*I 182·3	4	56·8				
		*F (*a*) 181·7	3	8·7	−0·6	0·287	0·8−0·7	−0·33
		F (*b*) 186·7	3	16·7	+4·4	1·987	0·2−0·1	+2·41
33	6·2	I 227·7	3	4·7				
		F (*a*) 228·0	3	8·0	+0·3	0·207	0·9−0·8	+0·13
		F (*b*) 227·5	4	121·0	−0·2	0·076	1·0−0·9	−0·09
32	6·1	I 243·0	4	82·0				
		F (*a*) 245·7	3	4·7	+2·7	1·012	0·4−0·3	+1·11
		F (*b*) 241·0	3	14·0	−2·0	0·814	0·5−0·4	−0·82
24	7·2	I 390·8	4	102·8				
		F (*a*) 395·0	3	54·0	+4·2	1·240	0·3−0·2	+1·07
		F (*b*) 393·0	3	122·0	+2·2	0·570	0·6−0·5	+0·56
8	7·4	I 451·0	4	150·0				
		F (*a*) 453·3	3	112·7	+2·3	0·549	0·7−0·6	+0·51
		F (*b*) 437·8	4	82·7	−13·2	2·176	0·1−0·05	−2·93
19	6·0	I 457·7	3	10·7				
		F (*a*) 450·3	3	153·7	−7·4	1·224	0·3−0·2	−1·62
		F (*b*) 457·7	3	44·7	0	—	—	0·00
12	5·7	I 531·0	3	74·0				
		F (*a*) 527·7	3	12·7	−3·3	0·872	0·5−0·4	−0·62
		F (*b*) 536·5	4	233·0	+5·5	0·919	0·4−0·3	+1·04
25	6·5	I 533·8	5	436·6				
		F (*a*) 529·0	3	104·0	−4·8	0·640	0·6−0·5	−0·90
		F (*b*) 545·3	3	8·7	+11·5	1·828	0·2−0·1	+2·15
21	5·9	I 582·0	3	32·0				
		F (*a*) 580·3	3	50·7	−1·7	0·269	0·9−0·8	−0·29
		F (*b*) 583·5	4	291·0	+1·5	0·244	0·9−0·8	+0·26
11	6·5	I 628·6	5	755·4				
		F (*a*) 633·3	4	708·8	+4·7	0·485	0·7−0·6	+0·75
		F (*b*) 640·4	5	859·2	+11·8	1·313	0·3−0·2	+1·87
10	6·4	I 632·8	4	486·8				
		F (*a*) 630·7	3	242·7	−2·1	0·228	0·9−0·8	−0·33
		F (*b*) 632·0	3	282·0	−0·8	0·085	1·0−0·9	−0·13
13	6·1	I 641·0	5	730·0				
		F (*a*) 642·3	3	12·7	+1·3	0·160	0·9−0·8	+0·20
		F (*b*) 646·3	3	4·7	+5·3	0·656	0·6−0·5	+0·83
20	6·0	I 655·8	4	523·6				
		F (*a*) 649·5	4	705·0	−6·3	0·623	0·6−0·5	−0·96
		F (*b*) 655·0	3	86·0	−0·8	0·095	1·0−0·9	−0·12

* I = initial. F = final (after incubation).

TABLE 7.—*Continued.*

Soil No.	pH.		Total N, p.p.m., Mean. ($\bar{x}$).	n+1.	S $(x-\bar{x})^2$	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	Gain or Loss of N in % of Total Initial N.
14	5·6	I	660·2	5	1040·6				
		F (*a*)	643·0	4	238·0	−17·2	1·897	0·1−0·05	−2·61
		F (*b*)	639·7	3	108·7	−20·5	2·028	0·1−0·05	−3·11
Do. washed	6·0	I	627·0	3	14·0				
		F	621·0	2	8·0	−6·0	2·427	0·1−0·05	−0·97
35	6·0	I	712·2	6	838·6				
		F (*a*)	717·3	3	25·7	+5·1	0·649	0·6−0·5	+0·72
		F (*b*)	716·7	3	85·7	+4·5	0·554	0·7−0·6	+0·63
Do. +$CaCO_3$	,,	I	711·9‡	(6)	(838·6)				
		F (*a*)	720·8	4	74·8	+8·9	1·290	0·3−0·2	+1·25
		F (*b*)	699·3	3	12·7	−12·6	1·654	0·2−0·1	−1·81
34	7·6	I	744·0	3	14·0				
		F (*a*)	741·7	3	52·7	−2·3	0·690	0·6−0·5	−0·31
		F (*b*)	749·0	3	54·0	+5·0	1·485	0·3−0·2	+0·67
7	5·1	I	745·3	3	12·7				
		F (*a*)	729·5	4	1937·2	−15·8	1·048	0·4−0·3	−2·12
		F (*b*)	724·0	4	1338·0	−21·3	1·658	0·2−0·1	−2·86
		(*a*)+(*b*):							
		60 d.	682·3	3	80·7	*−63·0*	15·97	*<0·01*	*−8·46*
15	5·4	I	753·3	3	140·7				
		F (*a*)	754·7	3	18·7	+1·4	0·272	0·8−0·7	+0·19
		F (*b*)	761·0	3	98·0	+7·7	1·221	0·3−0·2	+1·02
Do. washed.	5·9	I	709·7	3	182·7				
		F	709·0	3	26·0	−0·7	0·119	1·0−0·9	−0·10
23	7·6	I	754·0	3	62·0				
		F (*a*)	744·0	4	626·0	−10·0	1·116	0·4−0·3	−1·33
		F (*b*)	749·7	3	16·7	−4·3	1·203	0·3−0·2	−0·57
1	6·0	I	795·7	3	440·7				
		F	802·7	3	164·7	+7·0	0·697	0·6−0·5	+0·88
27	5·8	I	796·0	4	493·0				
		F (*a*)	785·0	3	42·0	−11·0	1·392	0·3−0·2	−1·38
		F (*b*)	790·0	3	18·0	−6·0	0·770	0·5−0·4	−0·75
22	5·8	I	815·7	3	52·7				
		F (*a*)	813·0	3	122·0	−2·7	0·199	0·9−0·8	−0·33
		F (*b*)	811·3	3	88·7	−4·4	0·071	0·4−0·3	−0·54
51+52†	6·4	I	816·0	4	170·0				
		F (*a*)	822·7	3	40·7	+6·7	1·355	0·3−0·2	+0·82
		F (*b*)	813·7	3	32·7	−2·3	0·473	0·7−0·6	−0·28

‡ Corrected for introduction of 6·8 p.p.m. N in the $CaCO_3$.

† Mixture of equal parts of samples.

6	5·6	I 825·5	4	657·0				
		F (*a*) 820·0	4	2040·0	−5·5	0·355	0·8−0·7	−0·67
		F (*b*) 835·3	3	10·7	+9·8	1·119	0·4−0·3	+1·19
		(*a*)+(*b*):						
		60 d. 806·0	3	416·0	−19·5	1·744	0·2−0·1	−2·36
29	7·6	I 969·3	4	224·8				
		F (*a*) 964·3	3	44·7	−5·0	0·892	0·5−0·4	−0·52
		F (*b*) 957·3	3	2·7	−12·0	2·384	0·1−0·05	−1·24
30	7·7	I 1071·7	3	48·7				
		F (*a*) 1074·0	3	104·0	+2·3	0·456	0·7−0·6	+0·22
		F (*b*) 1069·8	4	1160·6	−1·9	0·160	0·9−0·8	−0·18
2	6·5	I 1252·7	3	788·7				
		F 1261·0	3	1116·0	+8·3	0·466	0·7−0·6	+0·66
26	7·5	I 1272·3	3	308·7				
		F (*a*) 1258·0	3	234·0	−14·3	1·504	0·3−0·2	−1·12
		F (*b*) 1265·3	3	104·7	−7·0	0·843	0·5−0·4	−0·55
28	5·7	I 1582·0	4	534·0				
		F (*a*) 1578·0	3	378·0	−4·0	0·388	0·8−0·7	−0·25
		F (*b*) 1566·0	3	194·0	−16·0	1·777	0·2−0·1	−1·01
16	7·1	I 1594·5	4	211·0				
		F (*a*) 1599·7	3	160·7	+5·2	0·754	0·5−0·4	+0·33
		F (*b*) 1610·5	6	1019·5	+16·0	1·987	0·1−0·05	+1·00
44	7·4	I 1731·3	4	52·8				
		F (*a*) 1720·3	3	338·7	−11·0	1·628	0·2−0·1	−0·64
		F (*b*) 1732·7	3	88·7	+1·4	0·309	0·8−0·7	+0·08
17	6·2	I 1890·7	3	660·7				
		F (*a*) 1905·3	3	2444·7	+14·6	0·767	0·5−0·4	+0·77
		F (*b*) 1903·3	3	714·7	+12·6	0·995	0·4−0·3	+0·67
9	6·6	I 5859·0	3	5774·0				
		F 5847·0	4	25860·0	−12·0	0·189	0·9−0·8	−0·25

The results are very clear-cut. With one exception, the differences between nitrogen contents before and after incubation are generally small and cannot be regarded as indicating a significant change in the nitrogen content of the soil, since the values of P are all above 0·05. The exception is represented by the acid soil No. 7, which showed a significant loss of nitrogen after 60 days. Apart from this single instance we have 68 cases where the change in nitrogen content does not exceed the analytical error; this is true irrespective of soil type, humus content, reaction, and presence or absence of *Azotobacter*. Even where the numbers of *Azotobacter* are highest (Nos. 8, 35 + $CaCO_3$, and 44) there is no indication of any gain of nitrogen (cf. de' Rossi, 1932*d*). The last column of the table shows that the changes vary between +2·41 and −3·11% of the original nitrogen content. These values, however, are uncommon, and quite small changes are the general rule. In Figure 4 the frequencies of the percentage changes are arranged in groups of 0·4%. This grouping reveals an approximately binominal distribution around a mean value of −0·192% with standard deviation ± 1·162. This approximate normality further strengthens the evidence that the changes are mainly due to accidental experimental errors. The fact that the mean is somewhat below zero might suggest a tendency of the soils to lose small quantities of

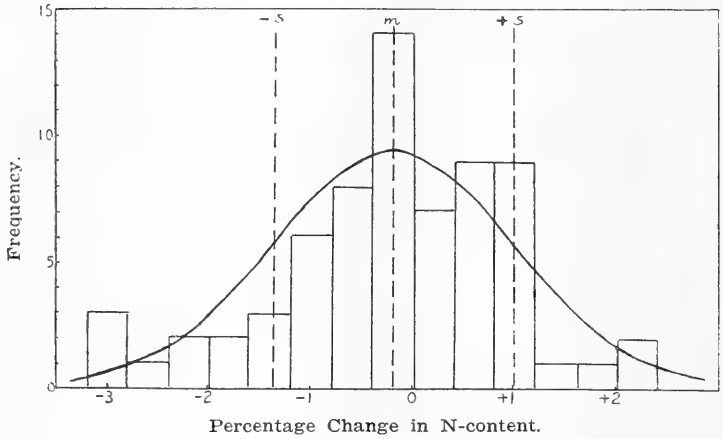

Fig. 4.—Distribution of percentage changes in nitrogen content of soils incubated without addition of organic matter (Table 7). *m*, mean; *s*, standard deviation. Theoretical curve of distribution constructed on the basis of Fisher's (1930) Table I.

nitrogen on incubation—losses which, although individually non-significant, might become significant in the aggregate. A closer inspection of the figures indicates that such small losses tend to be more common in definitely acid soils (pH 6·0 and less) than in the rest. In order to test whether this difference is apparent or real, the 68 percentage-values were divided into two groups (pH $\leqq$ 6·0, and pH $>$ 6·0), and the *t*-test of Fisher (1930, pp. 104–05) applied to decide whether the mean change in each group departs significantly from zero. For this test we calculate the standard deviation

$$s = \sqrt{\frac{S(x-\bar{x})^2}{n}}$$

$$\text{and } t = \frac{\bar{x}\sqrt{n+1}}{s}$$

The value of P is found, as before, from Fisher's Table iv. We have 40 data on soils of pH above 6·0; the calculation gives:

$n+1 = 40$. $\bar{x} = +0{\cdot}093$.
$s = \pm 1{\cdot}051$, $t = 0{\cdot}559$.
$n = 39$, P = 0·6–0·5 (not significant).

The same calculation on the 28 data on soil of pH 6·0 and less gives:

$n+1 = 28$. $x = -0{\cdot}56$.
$s = \pm 1{\cdot}237$, $t = 2{\cdot}395$.
$n = 27$, P = 0·05–0·02 (barely significant).

Although perhaps no very great importance should be attached to these figures, they show that in the faintly acid to alkaline soils the change in nitrogen content is insignificant, whereas in the definitely acid soils there is, if anything, an indication of small losses of nitrogen. That such a tendency to loss of nitrogen exists is also suggested by the fact that an unquestionably significant loss took place in the most acid soil (No. 7, pH 5·1) after prolonged incubation.

The numerous statements quoted above, concerning nitrogen fixation in soils incubated without addition of energy material, cannot thus in any way be confirmed in the case of the soils included in this series of experiments. When looking for an explanation for this contradiction, one cannot but notice that in most of the reports of gains of nitrogen under these conditions there are circumstances which make the reality of the gains appear doubtful. Firstly there is, as already mentioned, the possibility of an error due to analysis of dry soil before and moist soil after the incubation, as pointed out by Bal (1925). This, however, cannot offer a general explanation, since many authors state that dry soil was always analysed, and it is by no means all soils that show this effect (Olsen, 1937). Secondly there are many cases where the analytical error was not explicitly stated; although it is unlikely that this would be so severe as to cover changes of 10% of the nitrogen content or more, it may yet be an important contributing factor in producing fictitious gains of nitrogen, particularly if only two parallel determinations are made (Pfeiffer et al., 1906). Thirdly, some authors in the U.S.A. have used a modification of the Kjeldahl method (the "Official" method, as described in: Official and Tentative Methods of Analysis, by the Association of Official Agricultural Chemists, Ed. 5, 1935), in which the digestion is discontinued as soon as the acid is colourless, "or nearly so". In most other instances the time of digestion is not expressly stated, but it seems to be common practice to continue the heating only until the dark colour has disappeared (cf. Lemmermann, 1934). This is almost certainly insufficient to ensure complete conversion of the humus-nitrogen into ammonium sulphate, as shown by Christensen (1927), Ashton (1936), and Olsen (1937); in agreement herewith, Greaves and Greaves (1932) found that this procedure gave only 83% of the nitrogen found by the method of Dumas.[16] It might be concluded that changes in the proportion of nitrogen convertible into ammonium sulphate by short digestion might account for some of the apparent gains of nitrogen, which would automatically result if some of the humus nitrogen became more easily digestible during incubation of the soil. In order to test this possibility, 5 of the soils in Table 7 were re-analysed by the dry-digestion method with salicylic-sulphuric acid, digestion being stopped when the dark colour had gone (as in the "Official" method). The result are found in Table 8.

These nitrogen figures are all significantly lower than the corresponding figures found by "wet" digestion and prolonged heating. This is particularly noticeable in No. 26 (a heavy black loam; cf. Bal, 1925) and least marked in No. 44. In two cases, No. 29 and No. 44, there is actually a not very large, but still significant, difference in nitrogen content of soil before and after incubation. These differences would have impressed as actual gains of nitrogen if the soils had been analysed by this method only, but in view of the results in Table 7 they must be regarded as merely representing increases in the proportion of nitrogen convertible by short digestion (cf. Olsen, 1937, on the alleged nitrogen fixation by germinating seeds of leguminous plants).

Fourthly, in most of the experiments of Greaves (1914–16) and Greaves and Nelson (1923) the gains of nitrogen were reported as excess over sterile (presumably autoclaved) control soil. It has previously been shown, first by

[16] This method, indeed, may have a tendency to give too high values when applied to porous materials of a low nitrogen content like soil, as pointed out by Berthelot (1889); if it were not for this limitation, it would be highly desirable that this method should be used in exact experiments on nitrogen fixation in the soil.

TABLE 8.

Nitrogen-determination in Soils by Short-time Digestion.

Soil No.	Total N, p.p.m., Mean ($\bar{x}$).	n+1.	S $(x-\bar{x})^2$.	Gain (+) or Loss (−) p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	Recovery of N in % of "wet". Digestion (Cf. Table 7.)
34. Before incubation	660·3	3	660·3	—	—	—	88·8
Inc. 30 d.* ..	664·7	3	368·7	+4·4	0·300	0·8−0·7	89·2
51+52. Before incubation ..	754·5	2	12·5	—	—	—	92·5
Inc. 30 d. ..	751·0	2	32·0	−3·5	0·742	0·6−0·5	91·8
29. Before incubation	855·3	4	452·8	—	—	—	88·3
Inc. 30 d. ..	881·0	4	14·0	*+25·7*	4·124	*<0·01*	91·7
26. Before incubation	1008·7	3	554·7	—	—	—	79·3
Inc. 30 d. ..	999·7	3	448·7	−9·0	0·696	0·6−0·5	79·3
44. Before incubation ..	1641·0	4	270·0	—	—	—	94·8
Inc. 30 d. ..	1669·5	4	637·0	*+28·5*	3·278	*0·02−0·01*	96·7

* Mixtures of equal parts of samples (*a*) and (*b*) in Table 7.

TABLE 9.

Influence of Sterilization and Subsequent Incubation on Nitrogen Content of Soils.

Soil No. and Treatment.	Total N Mean, p.p.m. ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. due to		t.	P.
				Sterilization.	Incubation.		
15 (pH 5·4):							
Untreated ..	755·2	9	293·6	—	—	—	—
Autoclaved ..	725·7	3	162·7	*−29·5*	—	6·551	*<0·01*
Incubated ..	724·0	3	14·0	—	−1·7	0·460	0·7−0·6
28 (pH 5·7):							
Untreated ..	1576·0	10	1654·0	—	—	—	—
Autoclaved ..	1526·7	3	320·6	*−49·3*	—	6·077	*<0·01*
Incubated ..	1533·0	2	128·0	—	+6·3	0·564	0·7−0·6
64 (pH 6·4):							
Untreated ..	1822·0	3	182·0	—	—	—	—
Autoclaved ..	1825·3	3	130·7	+3·3	—	0·457	0·7−0·6
Incubated ..	1828·3	3	52·7	—	+3·0	0·543	0·7−0·6
30 (pH 7·7):							
Untreated ..	1071·7	10	1334·1	—	—	—	—
Autoclaved ..	1069·0	3	126·0	−2·7	—	0·316	0·8−0·7
Incubated ..	1032·0	3	152·0	—	*−39·7*	5·189	*<0·01*

Berthelot (1888), later by Pfeiffer et al. (1906) and Warmbold (1908), that sterilization as well as incubation of sterile soil may result in losses of nitrogen, which might represent still another source of error. A few experiments in this direction were carried out on 4 soils in Table 2. Portions of 50 gm. of moist soil were placed in 100 c.c. Erlenmeyer flasks and autoclaved for 45 minutes at 20 lb. pressure. One portion was analysed for total nitrogen immediately after the treatment, and another was analysed after incubation for 4 weeks at 28–30°C. Tests on nutrient agar slopes showed all the samples to be sterile both before and after incubation. The results are seen in Table 9. (It may here be remarked that the figures for "untreated" soil, except No. 64, are based on the total number of nitrogen determinations before and after incubation in Table 7; this must be considered permissible, since the changes in nitrogen content were never significant.)

The two strongly-acid soils, Nos. 15 and 28, lost significant quantities of nitrogen (3–4%) by autoclaving, but remained unaltered during incubation. The alkaline soil No. 30 was not affected by the autoclaving, but lost about 4% of its nitrogen during incubation, and finally the faintly-acid soil No. 64 remained unchanged by both sterilization and incubation. The loss of nitrogen as a consequence of sterilization is thus a common phenomenon, and if overlooked it may easily create the false impression of a gain of nitrogen in non-sterilized soil. For this reason too, as mentioned in the introduction, the statements of Greaves and co-workers (1928–32) on nitrogen fixation by numerous micro-organisms in sterilized soil cannot be accepted as valid, until it has been proved that the sterile control soil did not, like soil No. 30 in the present experiment, lose nitrogen on incubation.

The fact that spurious increases in the nitrogen content may be caused by incomplete conversion of the humus nitrogen into ammonia due to an insufficiently long digestion time as well as by the use of sterilized soil as control, combined in many cases with lack of information on the analytical error and uncertainty as to whether dry or moist soil was analysed, thus leads us to the conclusion that the occurrence of a measurable nitrogen fixation in soils incubated without addition of energy material must still be regarded as not proved with absolute certainty. Such claims can be accepted only when all the possible sources of error mentioned have been ruled out; this cannot be said to be the case in any of the experiments reviewed here, even in those that appear best documented (Remy, 1909, in whose data the occasional gains of nitrogen in soil with addition of $HgCl_2$ also suggest the operation of still other factors).

Besides this, the theoretical difficulties of explaining an intensive nitrogen fixation under these conditions are great. To take an example: in pure cultures of *Azotobacter* the yield of fixed nitrogen rarely, if ever, exceeds 1 part of nitrogen fixed per 16 parts of carbon consumed (= 25 mgm. N per gm. of glucose). If an ordinary soil containing 1% organic carbon gain only 50 p.p.m. nitrogen through the activity of *Azotobacter*, this will imply a consumption of *at least* 800 p.p.m. carbon, or 8% of the total carbon-content of the soil, by *Azotobacter* alone (cf. the estimate of Remy, 1909), which must derive the whole of its nitrogen supply from the atmosphere. In normal soils, however, the organic matter has a C/N-ratio in the neighbourhood of 10:1 (Waksman, 1932), and its decomposition is accompanied by production of ammonia and/or nitrate. It is difficult to see how this could be reconciled with a maximal nitrogen-fixing efficiency of *Azotobacter*, even if presence of molybdenum or vanadium compounds in the

soil might allow some fixation in the presence of nitrate (Bortels, 1936); in this connection it is interesting to note that Engel (1931*b*) found a C/N-ratio wider than 20:1 necessary for nitrogen fixation, and the depressing influence of nitrate on the development of *Azotobacter* in the soil is well known (Winogradsky, 1926). Further, we have assumed that the carbon compounds utilized by *Azotobacter* had the same value as glucose; it is extremely doubtful whether this assumption is justified, since the bulk of the soil "humus" is inaccessible to *Azotobacter*, which has to thrive on the organic by-products of the metabolism of other organisms. These by-products are likely to be mostly simple alcohols and organic acids (Winogradsky, 1932) of a lower energetic value per unit of carbon than glucose (Mockeridge, 1915; Gainey, 1928). It is thus necessary to strain the evidence badly in order to account for a nitrogen fixation of the order of some 5% of the total nitrogen content of the soil, unless we postulate *either* that *Azotobacter* functions in the soil in a manner totally different from that in pure cultures, *or* that unknown organisms with different properties act as nitrogen-fixers, none of which postulates is supported by experimental evidence.

These considerations, together with the experimental results, justify us in concluding that the claims of particularly vigorous processes of nitrogen fixation in soils from arid climates appear groundless so far as they are based on experiments of the type discussed here.

But even if wheat soils show no measurable increase in nitrogen content when incubated under conditions corresponding to those of bare-fallowing in summer time with good conservation of moisture, our problem is far from solved; we shall now turn to the question of the potential nitrogen-fixing capacity of the soils, as it is exhibited when an excess of directly available energy material is added.

2. *Soils with Addition of Glucose.*

That nitrogen fixation in soil may be stimulated to a marked extent by addition of directly assimilable carbonaceous food material, such as mannite or glucose, was shown first by Schneider (1906) and Koch et al. (1907), who found that up to 10–12 mgm. nitrogen could be fixed per gm. of glucose added to the soil. These investigations have been followed by a large number of contributions, which need not be reviewed in detail. Many of the authors quoted in the previous chapter have carried out experiments with addition of sugar to the soil, besides the experiments on soils incubated without addition of energy material. We may mention the papers of Remy (1909), Lemmermann and Blanck (1908), Lemmermann et al. (1910), Marr (1910), Koch (1909), Walton (1915), Greaves (1916), Traaen (1916), Hills (1918), Neller (1920), Greaves and Carter (1920), Meggitt (1923), Lander and Ali (1925), Zoond (1926), Christensen (1927), de' Rossi (1932*d*), Lemmermann and Themlitz (1934), Engel (1934), and Dhar (1937). Most of these investigations have shown that the maximal yield of fixed nitrogen under conditions favourable for the development of *Azotobacter* (good aeration, suitable temperature, neutral to faintly alkaline reaction, adequate supply of mineral nutrients, esp. phosphate) does not materially exceed 10–12 mgm. N per gm. of sugar or mannite. Statements of higher gains are comparatively few and not always convincing. Observations of this kind have been made by Brown and Smith (1912) in Iowa (in one instance a gain corresponding to 102 mgm. N per gm. mannite; misprint?), Greaves (1914) in Utah (up to 34 mgm. N per gm. mannite), Waksman and Karunakar (1924) in New Jersey (in

one instance 45 mgm. N per gm. mannite), Burgess (1932) in California (up to 27 mgm. N per gm. mannite), Turk (1936) in Michigan (up to 19 mgm. N per gm. mannite), and Bortels (1937) in Germany; the last author gives figures suggesting gains of 50–60 mgm. N per gm. glucose. It applies to all these statements, that the analytical procedure and the experimental error have not been reported in detail, and it is therefore entirely possible that some of the sources of error discussed in the previous chapter may have made some of the gains appear unduly high. It is noteworthy that Waksman and Karunakar, among whose data such a case appears, do not attach any great importance to these figures. Thus even the data from California, Utah, Iowa and Michigan cannot be said to prove that nitrogen fixation is more intensive in the soils from these arid or semi-arid districts than elsewhere.

Most of the research work in this direction has been of a chiefly chemical nature. Where bacteriological investigations have been carried out, they have usually shown that gains of nitrogen under aerobic conditions are associated with development of *Azotobacter*; this was first shown by Schneider (1906), Koch et al. (1907), and Remy (1909). Koch (1909) observed no gain of nitrogen in soils not containing *Azotobacter*, and in agreement herewith Waksman and Karunakar (1924) found no fixation in soil of pH below 6·0. Winogradsky (1925–26) showed that addition of assimilable carbon compounds results under favourable soil conditions in such a multiplication of *Azotobacter* that this organism altogether dominates the microscopic picture of the soil flora. He also observed that increasing concentrations of nitrate tend to counteract the development of *Azotobacter* by enabling other organisms to compete for the available energy material. No nitrogen determinations were made directly on the soils, but the "spontaneous cultures" of *Azotobacter* on silica-gel plates (Winogradsky, 1926–28) did not fix more than 10–12 mgm. N per gm. mannite; without development of *Azotobacter* there was no significant gain of nitrogen in these cultures, which led Winogradsky to the conclusion that this organism was alone responsible for nitrogen fixation in soil under aerobic conditions. A few authors (De and Pain, 1936; Turk, 1936) have reported nitrogen fixation in soils of acid reaction and said to be free from *Azotobacter*; since similar gains were observed in the same soils without addition of organic matter, these statements cannot be accepted as convincing.

Actual counts of *Azotobacter* in connection with nitrogen fixation experiments of this type have only been carried out in a few cases. The first step in this direction (apart from the semi-quantitative tests on lime plaques by Schneider, 1906, and Remy, 1909) seems to have been made by Hills (1918), who studied the influence of nitrate on cell multiplication and nitrogen fixation by *Azotobacter*—in both sterilized and untreated soil. Hills' results, however, have only a limited value, partly because the *Azotobacter*-counts and the nitrogen determinations were carried out in separate experimental series, but especially because the nitrogen figures are obviously faulty (as also pointed out by Zoond, 1926), owing to the use of dilute salicylic-sulphuric acid for the analysis, and consequent loss of NO_3–N (cf. Bristol and Page, 1923).[17] de' Rossi (1932*d*) carried out some highly interesting experiments, which showed that gains of 0·5–1·0 mgm. nitrogen in soil with addition of 2% mannite after 10–12 days at 32°C. were accompanied by the presence of 200 to 770 mill. *Azotobacter* (by plate count) at the end of the

[17] The loss of nitrogen in Hills' experiments thus need not be due to the physiological activity of *Azotobacter*, as suggested by Bonazzi (1921).

experiment. Although the data were few, there was some evidence of a correlation between amounts of nitrogen fixed and numbers of *Azotobacter*:

	mgm. N fixed in 5 gm. of soil.	*Azotobacter*, mill. per 5 gm. of soil.
Exp. IV, 5–	0·4 ..	373·9
,, IV, 7–	0·5 ..	401·9
,, V, 3–	0·5 ..	203·6
,, VI, 2–	1·0 ..	772·3

A remarkable series of investigations has been carried out in recent years in India by Dhar and co-workers (summarized by Dhar, 1937), who claim to have found evidence of a purely photochemical fixation of nitrogen; this process was stated to require a consumption of energy material similar to that in the biological fixation. In the latest series of experiments, Dhar (1937) compared soil samples with addition of various organic compounds, placed in sunlight and in the dark; periodical plate counts of *Azotobacter* and determinations of nitrogen and carbon were carried out; but neither the method of counting nor the analytical methods were clearly described. The counts of *Azotobacter* were regularly higher in soils incubated in darkness, where they often rose to several hundred millions per gm., but in soils exposed to sunlight the gains of nitrogen per unit of carbon disappeared from the soil were generally 50 to 100% higher than in the corresponding experiments in darkness. Dhar concludes from these results that "the nitrogen fixation in soils mixed with energy-rich materials is approximately 50% bacterial and 50% photochemical". This argument, however, seems altogether unconvincing. It is particularly important to notice that even the highest gain of nitrogen reported (15·7 mgm. per gm. of oxidized saccharose-carbon in soil exposed to sunlight for 3½ months) merely corresponds to a fixation of about 7 mgm. N per gm. of sugar consumed (or more precisely, converted into carbon dioxide and water; somewhat more must have been used for the production of bacterial substance); this could easily have been achieved by *Azotobacter* alone. That the counts of *Azotobacter* were lower under exposure to sunlight may find simple explanation in the entirely different temperature conditions; the soils in darkness were incubated at the optimal temperature of 28–33°C., whereas in the exposed soils the temperature must have fluctuated greatly and was sometimes reported to be as high as 48°C. It is highly probable that the recurrence of such high temperatures, together with the possible direct lethal action of the sunlight, would greatly accelerate the death-rate of the *Azotobacter*-cells and thereby prevent them from accumulating to the extent observed in the darkness-experiments, while renewed multiplication of *Azotobacter* might set in at night-time, and generally under less unfavourable temperature conditions; as an analogy, one might quote the experiments of Cutler and Bal (1926), who found that protozoa reduced the numbers of *Azotobacter* in solution cultures, but stimulated the rate of nitrogen fixation, presumably by decimating the bacterial population and thereby stimulating the production of new cells. Further, the numbers of *Azotobacter* stated to be present in the original soil were so high—2 to 12 mill. per gm.—that one might well doubt whether they were really all *Azotobacter* (cf. Dhar and Seshacharyulu (1936), as mentioned previously). Until more rigid proof is forthcoming, one cannot therefore regard the existence of photochemical nitrogen fixation as proved; and even if it were so, it does not appear from Dhar's data that the process would be more economical than the fixation by *Azotobacter*, so far as the consumption of energy material is concerned.

Nitrogen fixation experiments with sugar, etc., under anaerobic conditions have been comparatively few in number. The fixation is generally found to be less vigorous than under aerobic conditions, although it may reach some 5 to 6 mgm. nitrogen per gm. of sugar or mannite supplied, as shown by Traaen (1916), Greaves and Carter (1920), Turk (1936), and others quoted by Waksman (1932). The anaerobic conditions have mostly been produced simply by addition of an excess of water to the soil. Even if the saturation is not complete, the addition of sugar gives rise to an abundant development of vegetative clostridia, as shown by Winogradsky (1925–26), but on the other hand *Azotobacter* may still develop in fully water-saturated soil (Traaen, 1916).

A number of soils included in the present investigation were tested for nitrogen fixation on addition of glucose, chiefly under aerobic conditions. In the first series of experiments 16 soils from Table 2 were examined; mostly soils with a nitrogen content of less than 0·1% were selected, in order to be able to detect small changes with more certainty. The experiments were arranged exactly in the same manner as those without addition of organic matter (Table 7), and were carried out simultaneously with these. Altogether 2·5% of pure glucose[18] were added to the soil, 1·5% at start and 1·0% after 15 days. After 30 days' incubation at 28–30°C. the soil was air-dried and analysed for total nitrogen; some time, normally 4 to 5 days, after each addition of sugar, samples were taken for total microscopic counts of bacteria and for plate counts of *Azotobacter*; in some of the earlier experiments, before the plate method had been adopted in its final form, a loopful of soil suspension was simply streaked out on dextrine agar, or a number of soil particles were planted on silica-gel with mannite (Winogradsky, 1925).

Table 10 shows the results of the nitrogen determinations. As shown in the previous series of experiments, the nitrogen content of the soils never changed significantly during incubation without organic matter for 30 days, i.e. all determinations on the same soil before and after incubation may be regarded as belonging to the same population; therefore, the average of all these determinations may, as in Table 9, be regarded as the control with which the nitrogen content of the soil with glucose addition is to be compared. It is these general averages from the figures in Table 7 that are here given as "initial" nitrogen contents. Since these are based on nine or more parallel determinations, we get a considerably higher accuracy than by using only the actual initial nitrogen figures in Table 7. The significance of the differences was found as in the previous series, by means of the *t*-test.

Only soil No. 8, which is outside the wheat district, has pH 7·4 and had received an extra application of 0·2% $CaHPO_4$, shows a considerable gain of nitrogen. Although this gain appears large in proportion to the original nitrogen content (about one-third), it is actually only moderate, since it corresponds to a fixation of about 6 mgm. N per gm. of glucose added. In soil No. 25, a moderately productive wheat soil of pH 6·5, there is in one of the parallel dishes a small gain of nitrogen, equivalent to 10% of the original nitrogen content, or a fixation of 2·3 mgm. N per gm. of glucose. All other soils, irrespective of type, reaction, manurial treatment and presence or absence of *Azotobacter*, have entirely failed to fix nitrogen. Indeed, the addition of glucose has in many cases resulted in a significant loss of nitrogen; it is to be remembered that if some of the glucose

[18] On the basis of air-dry soil.

TABLE 10.

Nitrogen-fixation in Soils with Addition of 2·5 (=1·5+1·0)% Glucose.

Soil No.	Total N p.p.m., Mean ($\bar{x}$).	n+1.	S $(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m., ($\bar{x}_2-\bar{x}_1$).	t	P
24. Initial	392·7	10	310·1	—	—	—
Inc. plus glucose (*a*) ..	398·8	3	204·7	+6·1	1·355	0·3−0·2
(*b*) ..	381·3	3	162·7	*−11·4*	2·902	*0·02−0·01*
8. Initial	446·8	11	804·0	—	—	—
Inc. plus glucose (*a*) ..	595·7	3	160·7	*+148·9*	—	—
(*b*) ..	602·5	4	711·0	*+155·7*	—	—
19. Initial	455·2	9	315·2	—	—	—
Inc. plus glucose (*a*) ..	449·3	3	2·7	−5·9	1·570	0·2−0·1
(*b*) ..	453·7	3	12·7	−1·5	0·393	0·8−0·7
25. Initial	535·7	11	980·6	—	—	—
Inc. plus glucose (*a*) ..	592·7	3	448·7	*+57·0*	6·369	*<0·01*
(*b*) ..	523·3	3	82·3	−12·4	2·023	0·1−0·05
21. Initial	582·1	10	391·7	—	—	—
Inc. plus glucose (*a*) ..	586·7	3	4·7	+4·6	1·164	0·3−0·2
(*b*) ..	580·7	3	20·7	−1·4	0·347	0·8−0·7
10. Initial	631·9	10	1038·1	—	—	—
Inc. plus glucose (*a*) ..	633·0	4	654·0	+1·1	0·157	0·9−0·8
(*b*) ..	608·0	4	854·0	*−23·9*	3·217	*<0·01*
11. Initial	634·1	14	2718·6	—	—	—
Inc. plus glucose (*a*) ..	633·8	4	1332·6	−0·3	0·026	1·0−0·9
(*b*) ..	631·7	3	164·7	−2·4	0·272	0·8−0·7
14. Initial	649·3	12	2361·5	—	—	—
Inc. plus glucose (*a*) ..	639·7	3	40·7	−9·6	1·094	0·3−0·2
(*b*) ..	637·0	3	104·0	−12·3	1·384	0·2−0·1
20. Initial	653·1	11	1394·4	—	—	—
Inc. plus glucose (*a*) ..	638·3	3	138·7	−14·8	2·011	0·1−0·05
(*b*) ..	661·8	3	332·6	+8·7	1·114	0·3−0·2
7. Initial	731·8	11	4101·6	—	—	—
Inc. plus glucose (*a*) ..	699·0	4	1834·0	*−32·8*	2·689	*0·02−0·01*
(*b*) ..	713·7	3	1164·7	−18·1	1·326	0·3−0·2
23. Initial	748·7	10	892·9	—	—	—
Inc. plus glucose (*a*) ..	729·7	3	50·7	*−19·0*	3·116	*<0·01*
(*b*) ..	728·7	3	460·7	*−20·0*	2·735	*0·02−0·01*
15. Initial	755·2	9	293·6	—	—	—
Inc. plus glucose (*a*) ..	735·3	3	194·7	*−19·9*	4·933	*<0·01*
(*b*) ..	734·3	3	48·7	*−20·9*	6·182	*<0·01*
1. Initial	797·5	6	695·5	—	—	—
Inc. plus glucose ..	789·7	3	658·7	−7·8	0·792	0·5−0·4
6. Initial	827·1	11	2528·8	—	—	—
Inc. plus glucose (*a*) ..	801·3	3	620·6	*−25·8*	2·445	*0·05−0·02*
(*b*) ..	778·3	3	768·7	*−48·8*	4·520	*<0·01*

30. Initial	1071·7	10	1334·1	—	—	—
Inc. plus glucose (*a*) ..	1076·0	3	344·0	+4·3	0·529	0·7—0·6
(*b*) ..	1064·8	4	802·6	−6·9	0·874	0·4—0·3
2. Initial	1256·8	6	2004·6	—	—	—
Inc. plus glucose ..	1259·7	3	930·7	+2·9	0·200	0·9—0·8

Appendix: Soils with addition of Na_2MoO_4 or Na_2HPO_4 besides 2·0% glucose. Inc. 28 days.

10. Initial	631·9	10	1038·1	—	—	—
Inc. plus glucose alone ..	613·3	3	68·7	*−18·6*	2·817	*0·02—0·01*
Do. plus Na_2MoO_4 (*a*) ..	628·7	3	40·7	−3·2	0·491	0·7—0·6
(*b*) ..	622·7	3	74·7	−9·2	1·390	0·2—0·1
Do. plus Na_2HPO_4 (*a*) ..	672·3	3	162·7	*+40·4*	5·874	*<0·01*
(*b*) ..	663·3	3	164·7	*+31·4*	4·562	*<0·01*
30. Initial	1071·7	10	1334·1	—	—	—
Inc. plus glucose alone ..	1050·0	3	1178·0	*−21·7*	2·325	*0·05—0·02*
Do. plus Na_2MoO_4 (*a*) ..	1060·7	3	384·7	−11·0	1·471	0·2—0·1
(*b*) ..	1040·7	3	50·7	*−31·0*	4·197	*<0·01*
Do. plus Na_2HPO_4 (*a*) ..	1050·3	3	62·0	*−21·4*	2·887	*0·02—0·01*
(*b*) ..	1033·3	3	98·7	*−38·4*	5·110	*<0·01*

or its decomposition products persisted in the soil after incubation, a certain decrease in the nitrogen content would automatically result from the "dilution" of the soil with glucose. If no glucose at all were broken down to carbon dioxide and water (which of course will not happen), the resulting decrease would be 2·5% of the original nitrogen content, and this is frequently seen to be exceeded. It is noteworthy that such a loss has taken place also in the highly fertile, alkaline soil No. 30.

The microbiological examinations, recorded in Table 11, show a somewhat more complicated picture. The cultural tests show complete absence of *Azotobacter* in all soils of pH 6·0 and less (Nos. 19, 21, 14, 7, 15, 6), and even in the alkaline soils No. 23 and 24. Plates from the first of these showed a large number (about 2·5 mill. per gm.) of a fungus closely resembling *Dematium pullulans*, which has been claimed to fix nitrogen by Löhnis and Pillai (1908). This fungus and several other organisms from this experimental series were tested for nitrogen fixation with a negative result (Table 4). Soils No. 8, 10, and 11 show abundant growth of *Azotobacter* by qualitative tests. Plate counts show that in soil No. 25 the numbers of *Azotobacter* have risen to several millions per gm., highest in the dish where nitrogen was fixed, and even higher numbers are reached in soil No. 30, although no nitrogen was fixed here. The cultural tests thus merely show that nitrogen fixation coincides with multiplication of *Azotobacter*, which on the other hand may multiply to the order of many millions per gm. without any nitrogen fixation taking place.

The direct microscopic counts show some interesting features. A certain number of large globular organisms, 1·2–2·0μ in diameter, resembling *Azotobacter*-cells, were seen in practically all soils, but rarely in numbers exceeding some 4 to 5% of the total microflora. The only exceptions from this rule are represented by the soils where nitrogen fixation took place, viz., No. 8 and one of the parallels of No. 25, particularly the former, where the *Azotobacter*-like organisms occupy quite a dominant position, and where the fixation was most intense. Otherwise the microscopic flora appeared rather uncharacteristic; like the normal soil microflora (Thornton and Gray, 1934) it was composed mainly of small, short, non-

TABLE 11.

Microbiological Examination of Soils with Addition of Glucose.

Soil No. and Time of Examination.	Total Bacteria Direct Count. Mill. per gm.	*Azotobacter*-like Organisms. % of Total Bacteria.	*Azotobacter*-like Organisms. Mill per gm.	*Azotobacter* by Cultural Methods.	N Fixed, Mgm. per gm. Glucose.
24. Initial	—	—	—	M.S.: present.	—
Incubated:					
(*a*) 6 d. ..	577±51·0	2·0	(12)	D.A.: absent; after 6 d.:	Nil.
21 d. ..	482±52·0	3·1	(15)	numerous white bacterial	
(*b*) 6 d. ..	750±68·3	1·4	(11)	colonies; 21 d:	Nil.
21 d. ..	596±51·5	1·3	(8)	numerous fungi.	
8. Initial	—	—	—	D.A.: 9 per gm.	
Incubated:					
(*a*) 4 d. ..	—	—	—	D.A. and S.G.: abundant.	6·2
18 d. ..	4236±148	44·9	1900±112	Colonies of other	
(*b*) 4 d. ..	1770±90·1	21·2	353±37·4	organisms not con-	5·9
18 d. ..	3895±198	28·0	1090±81·8	spicuous.	
19. Initial	—	—	—	Absent.	—
Incubated:					
(*a*) 5 d. ..	1140±65·0	0·9	(10)	D.A.: absent; numerous	Nil.
20 d.	1303±82·5	0·5	(7)	fungi and spore-forming	Nil.
(*b*) 20 d. ..	1301±86·4	0·6	(8)	bacilli.	
25. Initial	—	—	—	M.S.: present.	—
Incubated:					
(*a*) 5 d. ..	2058±125	8·0	166±28·9	D.A.: 1·4 mill. per gm.	2·3
18 d. ..	3495±194	14·5	518±56·9	12·5	
(*b*) 7 d. ..	2303±147	5·9	137±28·1	7·0	Nil.
18 d. ..	1415±120	2·3	(33)	Absent.	
21. Initial	—	—	—	Absent.	—
Incubated:					
(*a*) 21 d. ..	—	—	—	D.A.: absent; numerous	Nil.
(*b*) 21 d. ..	—	—	—	fungi.	Nil.
10. Initial	—	—	—	D.A.: 20 per gm.	
Incubated:					
(*a*) 4 d. ..	1647±95·6	1·7	(27)	D.A. and S.G.: present;	Nil.
(*b*) 4 d. ..	1756±96·6	1·1	(19)	fungi numerous.	
11. Initial	—	—	—	M.S.: present.	—
Incubated					
(*a*) 4 d. ..	—	—	—	D.A. and S.G.: present;	Nil.
(*b*) 4 d. ..	1368±76·9	3·5	(58)	fungi numerous.	Nil.
14. Initial	—	—	—	Absent.	—
Incubated:					
(*a*) 5 d. ..	1634±114	1·2	(20)	D.A. and S.G.: absent;	Nil.
(*b*) 5 d. ..	1333± 89	1·8	(24)	numerous fungi and	Nil.
				spore-formers.	
20. Initial	—	—	—	Absent.	
Incubated:					
(*a*) 4 d. ..	—	—	—	D.A.: absent; numerous	Nil.
(*b*) 4 d. ..	—	—	—	fungi.	Nil.

23. Initial	—	—	—	M.S.: present.	
Incubated:				D.A.: absent; numerous	
(*a*) 8 d. ..	553±46·4	1·8	(10)	fungi, *Penicillium*, *Dematium* (?), after 21 d.	Nil.
21 d. ..	1267±82·4	3·4	(46)		
(*b*) 21 d. ..	540±45·0	1·2	(6)	*Trichoderma*.	Nil.
7. Initial	—	—	—	Absent.	
Incubated:				D.A. and S.G.: absent;	
(*a*) 6 d. ..	554±56·0	(0)	(0)	many fungi (*Penicillium*).	Nil.
(*b*) 6 d. ..	496±54·6	0·9	(4)		Nil.
15. Initial	—	—	—	M.S.: present.	
Incubated:					
(*a*) 5 d. ..	1673±111	1·5	(25)	D.A.: absent; numerous	Nil.
(*b*) 5 d. ..	1825±101	1·8	(33)	fungi, some big spore-formers.	Nil.
6. Initial	—	—	—	Absent.	
Incubated:				D.A. and S.G.: absent;	
(*a*) 6 d. ..	1094±94·9	3·1	(34)	many fungi and big	Nil.
(*b*) 6 d. ..	1092±83·0	4·9	(54)	spore-formers.	Nil.
30. Initial	—	—	—	M.S.: present.	
Incubated:					
(*a*) 5 d. ..	2297±177	7·2	166±38·8	D.A.: 2·1 mill. per gm.	Nil.
21 d. ..	3295±200	7·3	182±31·1	21·4	
(*b*) 5 d. ..	1883±140	2·3	(43)	2·7	Nil.
21 d. ..	3308±201	3·5	113±27·8	23·6	

Appendix: Soils with addition of Na_2MoO_4 or Na_2HPO_4 besides 2·0% glucose.

10. Glucose alone:					
5 d. ..	1038±68·5	2·2	(23)	D.A.: 1·9 mill. per gm.	Nil.
19 d. ..	483±47·9	4·2	(20)	absent.*	
Do. plus Na_2MoO_4:					
(*a*) 5 d.	1544±99·1	5·2	80·3±18·3	D.A.: >0·2 mill.	Nil.
19 d.	752±57·0	1·3	(10)	absent.*	
(*b*) 5 d.	1508±74·3	2·5	(38)	1·0 mill.	Nil.
19 d.	749±60·4	2·1	(16)	absent.*	
Do. plus Na_2HPO_4:					
(*a*) 4 d.	2476±163	16·9	370±47·8	D.A.: 174 mill.	2·0
28 d.	843±60·3	22·5	187±31·5	3·6 mill.	
(*b*) 4 d... ..	1494±97·9	32·8	487±50·2	>200 mill.	1·6
28 d.	928±62·8	11·0	107±19·6	absent.*	
30. Glucose alone:					
4 d.	1550±116	1·2	(19)	D.A.: 0·13 mill.	Nil.
18 d.	2419±153	5·3	127±26·9	37·1 mill.	
Do. plus Na_2MoO_4:					
(*a*) 4 d.	2641±149	1·1	(29)	D.A. 0·40 mill.	Nil.
18 d.	2109±147	5·3	114±27·3	35·2 mill.	
(*b*) 4 d.	—	—	—	0·17 mill.	Nil.
18 d.	1709±118	7·5	127±26·4	35·6 mill.	
Do. plus Na_2HPO_4:					
(*a*) 6 d.	1829±134	1·0	(18)	D.A.: 4·5 mill.	Nil.
32 d.	2494±195	6·2	156±37·6	57·0 mill.	
(*b*) 6 d.	1465±106	0·7	(10)	4·0 mill.	Nil.
32 d.	4333±268	5·1	218±39·9	51·5 mill.	

* All plates covered with green *Trichoderma*.

Abbreviations: D.A.: dextrine agar. M.S.: Beijerinck's mannite solution. S.G.: silicic acid gel plus mannite.

spore-forming rods and coccoid organisms, with occasional admixtures of larger rod-shaped bacteria, and mycelium and spores of fungi and actinomycetes. Some vegetative clostridia were seen in soil No. 25; otherwise these organisms were seen only very sporadically or mostly not at all.

It is somewhat surprising that no nitrogen fixation and no very conspicuous microscopic development of *Azotobacter* should take place in soils like Nos. 10, 11, 23, 24, and 30, of pH 6·4 to 7·7. A supplementary experiment was carried out with soils No. 10 and 30, in order to test whether this might be due to deficiency of phosphate or molybdenum. This experiment was carried out like the others, but with only 2% glucose (1% at start and 1% after 2 weeks), and with extra addition of: (*a*) nothing; (*b*) Na_2MoO_4 (No. 10: 13·3 p.p.m.; No. 30: 22·0 p.p.m.); (*c*) Na_2HPO_4 (No. 10: 0·03%; No. 30: 0·025%). The soils were incubated for 4 weeks, except No. 30 plus phosphate, which, due to external circumstances, was kept for 32 days. The results are given in the appendices to Tables 10 and 11.

The control soils with no addition besides glucose show exactly the same result as in the previous series: considerable multiplication of *Azotobacter* (by plate count), but no gain of nitrogen. Addition of molybdate affects neither the *Azotobacter*-counts nor the nitrogen-figures significantly; the lack of fixation thus does not appear to be due to molybdenum deficiency. In soil No. 10 the addition of phosphate stimulates the development of *Azotobacter* very markedly, as shown by both the direct and the plate counts, and a significant gain of nitrogen takes place, corresponding, however, to a fixation of only 1·6–2·0 mgm. N per gm. of glucose. In comparison herewith it is surprising to see that in soil No. 30 the addition of phosphate has only stimulated the multiplication of *Azotobacter* slightly and has not resulted in any nitrogen fixation (indeed, there is a significant loss of nitrogen). Some still unknown inhibitory factor seems to be operating here;[19] it is perhaps of some significance that that strain of *Azotobacter* which proved ineffective when first tested for nitrogen fixing capacity (Table 4), was isolated from this soil.

It is a highly important fact that *Azotobacter* may multiply to the extent of several millions per gm. of soil (by plate counting) without causing any measurable gain of nitrogen. In comparison with such numbers the few thousand *Azotobacter* per gm., which usually represent the maximum under natural soil conditions, would appear altogether insignificant (cf. de' Rossi, 1932*c*). Things might indeed be different, if the colonies in counts from natural soil should arise, not from individual cells, but from aggregates of thousands or even millions of cells. This, however, is hardly the case; in shaken soil suspensions the *Azotobacter*-like cells certainly may appear in clumps, but these are not normally of an extraordinary size (Winogradsky, 1925; Thornton and Gray, 1934), and the same even seems to be the case in undisturbed soil as shown by the contact-slide method (Rossi et al., 1936;[20] Starkey, 1938); moreover, these cells are not necessarily all *Azotobacter* (cf. Dianowa and Woroschilowa, 1931; Rossi et al., 1936). If the multiplication of *Azotobacter* is stimulated by addition of assimilable organic matter, most cells are found to occur singly or in very small aggregates (Winogradsky, 1926); this was also the case in the present experiments, as

[19] It can hardly be a question of the "weather-factor" (Stapp and Bortels, 1936), since this experiment was carried out simultaneously with the same on soil No. 10, in which nitrogen fixation took place.

[20] According to these authors, the bacterial "clusters" rarely contain more than about 30 individuals.

shown by the characteristic photographs (Pl. i, figs. 3–5). A comparison between the plate counts of *Azotobacter* and the corresponding direct counts of *Azotobacter*-like cells, where the latter are sufficiently numerous to be counted with a reasonable accuracy (more than 80 mill. per gm.) shows the following relationship:

Soil No.	Plate Count. Mill. per gm.	Direct Count. Mill. per gm.	Plate Count in % of Direct Count.
25 *a*, 5 d.	1·4	166	0·8
18 d.	12·5	518	2·4
b, 5 d.	7·0	137	5·1
30 *a*, 5 d.	2·1	166	1·3
21 d.	21·4	182	11·7
b, 21 d.	23·6	113	20·9
10+Mo, *a*, 5 d.	0·2	80	0·25
$+P_2O_5$, *a*, 4 d.	174·0	370	47·0
28 d.	3·6	187	1·9
b, 4 d.	(>200·0)	487	(>40·0)
30 (sec. exp.), 18 d.	37·1	127	29·2
+Mo, *a*, 18 d.	35·2	114	30·9
b, 18 d.	35·6	127	28·0
$+P_2O_5$, *a*, 32 d.	57·0	156	36·5
b, 32 d.	51·5	218	23·6

Thus in 8 cases out of 15 the plate method shows figures from one-fifth to nearly one-half of the total number of *Azotobacter*-like cells. Since their numbers are highest where nitrogen fixation has taken place and where the plate method also shows high numbers of *Azotobacter*, and since the percentage of *Azotobacter*-cells capable of developing into colonies on agar may be as low as a few per cent. (Beijerinck, 1909), we may tentatively assert that high direct counts of *Azotobacter*-like cells in the soils here dealt with are represented chiefly by actual *Azotobacter*-organisms.

We can now make a rough estimate of the quantity of nitrogen contained in the cell-substance of these organisms. If we assume that the *Azotobacter*-cells have an average volume of $5\mu^3$ [21] and a specific gravity of 1, and contain 20% dry matter with 10% nitrogen (Burk and Lineweaver, 1930), 1000 mill. cells will represent 0·1 mgm. N. If we compare the quantities of nitrogen actually fixed with the estimated nitrogen-contents of the highest numbers of *Azotobacter*-like cells observed, we find the following:

Experiment No.	Highest Count of *Azotobacter*-like Cells. Mill. per gm.	Nitrogen in Cells, p.p.m. (Calc.).	Total Nitrogen Fixed. p.p.m.	Cell-N in % of Fixed Nitrogen.
8 *a*	1,900	190	149	128
8 *b*	1,090	109	156	70
25 *a*	518	52	57	91
10+phosphate *a*	370	37	40	93
b	487	49	31	158

[21] Unfortunately, it is impossible to measure the size of the living *Azotobacter*-cells in the soil. A number of measurements of these cells on the slides from soils No. 8, 10 and 25 showed an average diameter of 1·7-1·8μ, corresponding to a cell volume of 2·5-3·0μ^3. Some shrinking, however, is caused by the drying and staining. Some tests on pure cultures of *Azotobacter* showed that the same method of staining as used in the direct counts caused the cells to shrink to about 60-70% of their volume in a living condition.

There is here the same rough proportion between numbers of *Azotobacter* and gains of nitrogen as in the experiments of de' Rossi (1932*d*) and, considering the wide margins of error, the quantities of nitrogen in the *Azotobacter*-like cells are remarkably similar to the actual gains of nitrogen. This suggests strongly that where nitrogen fixation has taken place, it has consisted in a synthesis of *Azotobacter*-cells, i.e. the process is under these conditions "growth-bound" as in pure cultures.

Admittedly a certain proportion of the cell nitrogen may have been derived from the soil and not from the atmosphere, but against this must be set the nitrogen contained in those generations of *Azotobacter*-cells that have arisen and disappeared again before the time of counting, as well as possible subsequent generations—a quantity which we cannot estimate with any accuracy, since we do not know the rates of death and reproduction of *Azotobacter*-cells in the soil.

If the nitrogen-fixation consists in a simple synthesis of *Azotobacter*-cells, it is not surprising that this organism may multiply vigorously without causing any significant fixation; for instance, a production of 50 mill. *Azotobacter*-cells per gm. of soil, deriving all their nitrogen from the atmosphere, would give an increase of only 5 p.p.m. of nitrogen—a quantity difficult or impossible to detect in a soil of normal nitrogen content. The assimilation of combined soil nitrogen must also be reckoned with; every p.p.m. of nitrate- or ammonia-nitrogen taken up by *Azotobacter* would suffice for the production of about 10 mill. cells per gm. of soil.

All soils from these experiments were tested qualitatively for nitrate and ammonia at the termination of the experiment. Apart from one exceptional case, nitrate was always absent, but small quantities of ammonia-N (2–3 p.p.m. by quantitative determination) were sometimes found. The exception was represented by soil No. 8, which contained the following quantities in p.p.m.:

	NO_3–N.	NH_4–N.	Total.	Increase.
Before incubation ..	3·7	6·8	10·5	—
After incubation (*a*) ..	7·4	11·7	19·1	8·6
After incubation (*b*) ..	24·1	5·6	29·7	19·2

The increases correspond to 6 and 12% respectively of the amounts of nitrogen fixed (149 and 156 p.p.m.). Apparently the glucose has been used up very quickly, after which the fixed nitrogen may undergo a rapid mineralization, as shown by Engel (1934; cf. also Burk and Horner, 1936).

As a supplement to the nitrogen fixation experiments in Table 11 with addition of phosphate, a number of soils were tested qualitatively for their ability to support an abundant *Azotobacter*-flora with and without addition of phosphate. These experiments were carried out by the soil-plaque method of Winogradsky (1926): to 50 gm. of air-dry soil were added 5% starch, 1% $CaCO_3$, 5 c.c. 0·01% solution of Na_2MoO_4, and sufficient distilled water to give the mixture the consistency of a firm paste, which was moulded into a plaque with a smooth surface in an ordinary Petri dish; similar plaques were given an extra addition of 0·2% $CaHPO_4$. To ensure presence of *Azotobacter*, each plaque was inoculated with 0·5 c.c. of a thin suspension (just visible turbidity) of a pure culture of *Azotobacter*, of which the same strain was used in all cases (the inoculation

principle of Christensen, 1915, as also applied by Ziemecka, 1932). The plaques were incubated at 28–30°C. and watched for macroscopic growth of *Azotobacter*, which, where present, became visible after 2 days and did not increase perceptibly after 4–5 days' incubation. Altogether 50 soils (46 wheat soils) were tested, in duplicate where sufficient soil was available. The results are seen in Table 12, where the amount of growth is indicated by the following characters:

0 : no visible growth of *Azotobacter*.
I : very thin growth of small confluent *Az.*-colonies.
II, III : amounts of growth intermediate between I and IV.
IV : maximal growth (thick slimy layer of *Azotobacter*).

Fig. 5.—Development of *Azotobacter* on soil plaques. (Soil No. 29, inc. 5 d. 28-30°C.) Left: without phosphate (no visible growth of *Azotobacter*); right: with phosphate (maximal growth of *Azotobacter*). (⅔ nat. size.)

Figure 5 shows a good example of negative (0) and maximal (IV) development of *Azotobacter*. In some instances only a few isolated *Azotobacter*-colonies appeared instead of a confluent growth; in these cases the number of colonies is reported in the table. Without phosphate addition only one soil (No. 44, outside the wheat belt) gave a good growth, which was not further increased by phosphate addition, and only one wheat soil (No. 81) gave a fair growth without phosphate addition (incidentally, these two soils were among the richest in *Azotobacter*; cf. Table 2). Of all other soils, only a few gave a scanty growth without phosphate addition, and most of them none at all. When phosphate is added, the growth of *Azotobacter* becomes fair to excellent, except in a few cases (Nos. 11, 38, 65, and 82), where a stimulating effect of the phosphate is still often noticeable. This simple experiment thus shows that, even with addition of sufficient energy material, lime and molybdenum, practically all wheat soils here examined contain insufficient phosphate for a vigorous development of *Azotobacter*. It is interesting to observe that this applies also to highly productive soils like Nos. 26–29, 61, 62, 65, 66 and 68. This pronounced phosphate deficiency seems fully to explain why

TABLE 12.

Influence of Phosphate on Development of Azotobacter *on Soil Plaques.*

Soil No.	Growth of *Azotobacter.*	
	$-P_2O_5$.	$+P_2O_5$.
2	0	II
6	I	II
7	0	II
	0	II
11	0	(11 col.)
12	0	III
	0	III
13	0	III
	0	III
14	0	III
	0	III
15	0	0
22	0	II
25	0	II
26	0	IV
	0	IV
27	0	II
	0	II
28	0	II
	0	II
29	0	IV
	0	IV
31	0	III
	0	III
34	0	III
38	0	(7 col.)
42	0	III
	0	III
*44	III	III
45	0	II
	0	II
46	0	II
	0	II
47	0	III
	0	III
48	0	III
	0	III
51+52	(1 col.)	II
53+54	I	II
*55+56	0	II
58	0	III
*59	0	III
	0	III
*60	0	III
	0	III
61	0	IV
62	0	IV
63	0	IV
	(2 col.)	III
64	I	II
65	0	(1 col.)
	0	(36 col.)
66	0	III
67	0	II
68	(1 col.)	II
	(3 col.)	II
69	0	IV
74	0	III
	0	III
75	0	II
	0	II
76	0	II
	0	III
77	0	II
	0	II
78	0	II
	(3 col.)	II
79	0	II
	0	III
80	0	II
81	II	IV
82	0	(44 col.)
83	0	III
84	0	III
85	0	II

Soils marked * are outside the wheat belt.

approximately neutral to alkaline soils like Nos. 10, 11, 23, 24, and 30 failed to fix nitrogen on addition of glucose.

Nitrogen fixation experiments under anaerobic conditions were carried out on a small scale only. The first experiment was made on soil No. 21. Portions of 50 gm. air-dry soil were placed in small glass cylinders with glass lids, and received additions of 1·5% glucose, 1·0% $CaCO_3$, 0·004% Na_2HPO_4 (in solution), and 28% H_2O, which made the soil completely water-saturated. Two parallels were set up, and a glass slide was placed vertically in the middle of the soil column in each glass. The glasses were incubated at 28–30°C.; the slide in glass *a* was removed after 3 days and the one in glass *b* after 7 days, at which time the experiment was terminated, and microscopic counts and nitrogen determinations carried out. Gas formation was visible after 2–3 days. Plate counts after 7 days showed in both glasses a certain development of *Azotobacter*, which numbered 0·6–0·9 mill. per gm. (cf. Traaen, 1916). The next experiment was therefore carried out in the absence of oxygen. Two soils were used: (1) No. 30, with 1·5% glucose and 40% of a solution containing 0·05% Na_2HPO_4; and (2) No. 58 after previous incubation for 30 days and washing until free from nitrate (in order to have a soil of a low nitrogen content and free from mineral nitrogen); to this were added 1·5% glucose, 1·0% $CaCO_3$, and 21·4% of the same solution of Na_2HPO_4. The soil samples were placed in 100 c.c. glass beakers in a desiccator of about 1 litre capacity, where the oxygen was absorbed by means of pyrogallic acid and NaOH. The experiment was terminated after 7 days at 28–30°C.; gas formation and smell of butyric acid were also noticeable here. The results are seen in Table 13. (It should be pointed out that the initial nitrogen content of soil No. 58 is somewhat higher than should be expected after the washing out of the nitrate; this is due to the circumstance that the batch of calcium carbonate, although labelled "purissimum", was found to contain no less than 0·068% N; consequently the addition of 1·0% $CaCO_3$ adds 6·8 p.p.m. N to the soil.)

TABLE 13.

Nitrogen-fixation in Soils with 1·5% Glucose under Anaerobic Conditions.

Soil and Period of Incubation.	Total N, p.p.m., Mean ($\bar{x}$) (Catalyst : Se.).	n+1.	$S(x-\bar{x})^2$.	Gain of N, p.p.m., ($\bar{x}_2-\bar{x}_1$).	t.	P.
21. (+$CaCO_3$) Initial ..	582·8	9	352·0			
Inc. 7 d. (*a*).. ..	606·3	3	4·7	*23·5*	5·902	*<0·01*
(*b*) ..	592·0	4	204·0	9·2	2·153	0·1–0·05
58. (+$CaCO_3$) Initial ..	547·5	4	147·0			
Inc. 7 d.	608·0	6	766·0	*60·5*	8·774	*<0·01*
30. Initial..	1071·7	10	1334·1			
Inc. 7 d.	1124·0	4	298·0	*52·3*	7·580	*<0·01*

Direct counts : No.	Total Bacteria. Mill. per gram.	Vegetative Clostridia. Mill. per gram.
21. Inc. 3 d. (*a*) ..	447±30·0	148±15·9
7 d. (*a*) ..	480±32·3	123±14·6
(*b*) ..	625±43·8	177±20·6
58. Inc. 7 d. ..	1276±74·0	663±47·1

In soil No. 21, which had been in contact with the air, the gain of nitrogen is significant only in glass *a*, and corresponds to a fixation of only 1·5 mgm. N per gm. glucose. In the other two soils the gains are higher, corresponding approximately to fixation of 3·5–4 mgm. N per gm. glucose, which is comparable to the yield in a vigorously fixing pure culture of *Clostridium pasteurianum*. The contact slides in soil No. 21 showed an abundance of big and typical clostridia, which stained particularly well after 3 days, but were more abundant, although largely Gram-negative, after 7 days. (See fig. 7, Pl. i.) The direct counts from soil No. 30 were lost by an accident; in the other two soils, organisms of the type of *Cl. pasteurianum* dominated the microscopical picture entirely. This is especially true of soil No. 58, where the fixation was stronger, and where the clostridia account for about one-half of the number of all the bacteria present; but if we consider their comparatively large cell-size, it becomes obvious that they account for much more than one-half of the total bulk of bacterial protoplasm present. Their variable and irregular shape and size make it very difficult to estimate their average cell-volume, but it is probably not far out to regard the average mature cell before sporulation as a cylinder of 1μ diameter and 5μ length, which corresponds to a volume of approximately 4μ^3. If we assume a content of 20% dry matter with 10% nitrogen, 1000 mill. cells will represent 0·08 mgm. N, and a calculation similar to the previous for *Azotobacter* gives:

Soil No.	Total Number of Clostridia, Mill. per gm.	Cell–N, p.p.m. (Calc.).	Total N Fixed, p.p.m.	Cell–N, % of Fixed N.
21 *a*, 3 d.	148	11·8	23·5	50
7 d.	123	9·8		42
21 *b*, 7 d.	177	14·2	(9·2)	—
58, 7 d.	663	53·0	60·5	88

These figures, although admittedly very roughly approximate, suggest that this process of fixation also consists in a simple synthesis of bacterial cells. If this is so, it seems unlikely that the process should be highly important under natural conditions in field soils, where vegetative clostridia are hardly ever present in numbers sufficient to be detected by microscopic methods.

We may now summarize the results of the experiments in this chapter:

Wheat soils with addition of glucose show, under aerobic conditions, only a very slight nitrogen-fixing capacity, and in most cases none at all, even if the soil reaction is favourable for the growth of *Azotobacter*. If nitrogen fixation takes place, it is accompanied by a development of *Azotobacter*, which does not multiply in soils of pH 6·0 and less, and may even fail to develop at higher pH-values, owing to phosphate deficiency. The process of fixation seems to consist in a simple synthesis of *Azotobacter*-cells, of which some 10 mill. per gm. of soil must be expected as required for the fixation of each p.p.m. of nitrogen. On the other hand, a multiplication of *Azotobacter* to a level incomparably higher than ever found under natural conditions (several millions per gm.) may take place without being accompanied by any measurable gain of nitrogen. The absolute lack of nitrogen fixation where no multiplication of *Azotobacter* has taken place proves conclusively that other types of organisms do not function as nitrogen-fixers in these soils under the conditions at hand. Nothing in the present results indicates

that special types of *Azotobacter*, such as those described by Altson (1936) and Starkey and De (1939), display any activity in acid soils.[22]

If nitrogen fixation is induced under anaerobic conditions, even the moderate gain of 3–4 mgm. of nitrogen per gm. of glucose is accompanied by a domination of the microscopic picture by vegetative clostridia.

Although these experimental results do not favour non-symbiotic nitrogen fixation as an important phenomenon in the wheat soils, we cannot, without reservation, generalize to apply them to field conditions, where such abnormally large concentrations of sugar are never present,[23] and where straw and root material of higher plants, especially wheat, represent the bulk of the organic matter added to the soil. The decomposition of these materials would evidently be accomplished by a microflora of a composition entirely different from that in the glucose experiments, and possibly including nitrogen fixing organisms unable to act in the presence of high concentrations of glucose. Also the behaviour of *Azotobacter* might under these conditions possibly be different from that in the glucose experiments. (An interesting experiment by Marr (1910) suggests that addition of straw to the soil may cause a much larger gain of nitrogen than addition of sugar.) We shall now see how the addition of such complex plant materials affects the nitrogen-fixing microorganisms and the nitrogen content of the soil.

3. *Soils with Addition of Straw, etc.*

Natural plant materials as sources of energy for nitrogen-fixing bacteria have been the subject of much research work with both pure and mixed bacterial cultures as well as with the soil itself.

The first experiments in this direction were due to Gerlach and Vogel (1902), who tried straw and green mustard as food substances for pure cultures of *Azotobacter*, with negative results. Dvorak (1912, cit. after Fulmer, 1917) found that several kinds of leaves, straw and clover contained substances that could be utilized for nitrogen-fixation by *Azotobacter*. Fulmer (1917) found only a slight nitrogen fixation by *Azotobacter* in solution with green clover and wheat, and Waksman and Hutchings (1937) found no fixation at all in sterile straw inoculated with *Azotobacter*. The results of such experiments must necessarily vary with the composition of the plant material, and they have only a limited significance, since most of the organic matter of (esp. mature) plants is represented by compounds that are not directly available to *Azotobacter* or *Clostridium pasteurianum*, but which may become so when partly broken down by other microorganisms. Among these compounds, celluloses and hemicelluloses occupy the first place; whether decomposition products from the lignins can serve as food

[22] The present author has not so far (Jan., 1940) been able to detect the presence of acid-resistant types of *Azotobacter* (*Az. indicum* Starkey and De) in Australian soils.

[23] Except perhaps where sugar or molasses has been added to the soil. Counts of *Azotobacter* in field soils under such treatment do not seem to have been carried out except in recent work in India by Dhar and Seshacharyulu (1936). The numbers of *Azotobacter* which they report in molasses-treated soil seem, however, quite fantastic—in certain instances 28,000 mill. per gm. of soil (by plate counting; the actual number of cells must have been at least a little higher). Assuming as before that 1000 mill. cells represent 0·1 mgm. N, this number of *Azotobacter*-cells alone would give the soil a nitrogen-content of 0·28%, whereas the actual *total* nitrogen-content was only about 0·1%! A misprint or miscalculation must be involved, unless, indeed, it be assumed that the *Azotobacter*-colonies originated from ultramicroscopic cell types; but the existence of these is still a matter for discussion.

material for nitrogen fixation is unknown, but does not appear likely, in view of the extreme slowness with which these compounds are decomposed.

Beijerinck (1904, cit. after Waksman, 1932) was the first to show that cellulose can serve for fixation of nitrogen in a crude culture of *Azotobacter* and anaerobic cellulose-decomposing bacteria. Pringsheim (1910) demonstrated the same phenomenon in mixed cultures of *Azotobacter* or *Cl. americanum* combined with anaerobic cellulose-decomposing bacteria;[24] the clostridia especially showed a much stronger nitrogen fixation than in ordinary pure cultures, in some cases no less than 12 mgm. N per gm. of cellulose decomposed. In combinations of *Azotobacter* and crude cultures of aerobic cellulose-decomposing bacteria, Hutchinson and Clayton (1919) found gains of up to 19 mgm. N per gm. of decomposed cellulose; this figure, indeed, may be too high; even the largest actual gain of nitrogen, about 5·6 mgm. per 50 c.c. of solution, could have taken place at the expense of the 0·5 gm. mannite also present; it may be that metabolic by-products of the cellulose-decomposing bacteria have stimulated *Azotobacter* to utilize the mannite more effectively than in the pure cultures, where the gains of nitrogen look remarkably low, or nitrogen may have been lost as ammonia from the pure *Azotobacter*-cultures during the long period of incubation (cf. Burk and Horner, 1936). Bucksteeg (1936) was unable to confirm these results with pure cultures of aerobic cellulose-decomposing bacteria, although crude cultures gave some fixation. Krishna (1928*b*) found only very small or negative gains of nitrogen in various combinations of nitrogen-fixing and cellulose-decomposing bacteria on both cellulose and straw (cf. Waksman and Hutchings, 1937). When cellulose is added to the soil and attacked by the natural soil microflora, its decomposition may result in large gains of nitrogen. Koch (1910) found that up to 10 mgm. N could be fixed per gm. of cellulose decomposed, but this depended largely on the nature of the cellulose-decomposing organisms. Engel (1931*b*) and Bucksteeg (1936) reported gains of 5–7 mgm. N per gm. of cellulose added to the soil, but did not determine the actual quantity of cellulose transformed. Engel found that a C/N ratio wider than 20/1 was necessary for nitrogen fixation. On the other hand, Vandecaveye and Villanueva (1934) found large gains of nitrogen in soils with addition of 1% filter paper to which had been added sufficient $NaNO_3$ to give it a content of 2·5% N; the C/N ratio of soil + filter paper and $NaNO_3$ was 10·2–13·6:1. The experiments are interesting because carbon determinations were also carried out, but the results look astonishing; for instance, in one case there is reported a gain of 532 p.p.m. nitrogen with a corresponding loss of 0·08%, or 800 p.p.m., carbon (Table 4, manured soil + lime and filter paper), i.e. 1 unit of N fixed per 1·5 units of C lost as carbon dioxide! This would be a nitrogen fixation of unparalleled economy, but one's confidence in the validity of the results becomes badly shaken by the circumstance that an almost equally high gain of nitrogen was reported in soil without any addition of organic matter.[25] It also appears surprising that such gains should have taken place although the numbers of *Azotobacter*, as determined by the silica-gel method, never exceeded 15,000 per

[24] It may be open to doubt whether methane fermentation of cellulose is actually due to pure cultures.

[25] Even more surprising is the circumstance that in one case (Virgin Palouse silt loam) in Vandecaveye and Villanueva's Table 4 the carbon content is actually stated to be *higher* after incubation than before, although the graph in Fig. 2 shows a vigorous CO_2-production. It is impossible to avoid the conclusion that some kind of sampling error must have influenced the results.

gm. The authors suggest the possible activity of organisms of the type studied by Greaves and co-workers (1928–32).

Hemicelluloses have not been studied much in this respect. Pringsheim and Pringsheim (1910) found that agar could be utilized by *Azotobacter* and *Cl. americanum* in combination with *Bact. gelaticum*. As in the experiments with cellulose, the clostridia displayed a remarkably great activity, and fixed up to 26 mgm. N per gm. of agar decomposed. It would seem that the nitrogen metabolism here is quite different from what happens in pure cultures of clostridia; Pringsheim's experiments, unfortunately, were few in number, and the whole problem urgently needs re-investigation. Koch (1909) found no gain of nitrogen in soil with addition of xylan. Diehm (1932) tried various hemicelluloses in soil experiments and found a sometimes very vigorous nitrogen fixation; the maximal gain corresponded to 31 mgm. N per gm. of galactan decomposed; the methods were not described in detail.

Straw and other natural plant materials have been studied much more extensively, especially in soil experiments. Koch et al. (1907) found no altogether conclusive evidence of nitrogen fixation in soil with addition of barley straw and no fixation, or loss, with filter paper, buckwheat or mustard hay. Remy (1909) found losses of nitrogen in soil with mustard plants or farmyard manure. Marr (1910) observed a large initial gain of nitrogen (corresponding to 8·8 mgm. per gm. of straw supplied) in soil with 0·5% straw, but this was followed by a loss of nitrogen on further incubation; addition of sugar gave rise to a much less intensive fixation. Tottingham (1916) and Richards (1917) observed nitrogen fixation in fermenting manures, even where *Azotobacter* did not appear to be present. Fulmer (1917) found only small gains of nitrogen in soils with green clover, wheat, or oats. Hutchinson (1918) found variable gains of nitrogen in soil with different kinds of leaves and straw; the maximum was about 6 mgm. N per gm. of straw in a sand-soil-mixture. Murray (1921) reported quite extraordinary gains of nitrogen,[28] even when ammonium sulphate was also added, and apparently independent of the quantity of straw added to the soil; similar gains were reported in soil without straw altogether, which makes the statement appear somewhat dubious. Meggitt (1923) found no gain of nitrogen on addition of straw to a soil that fixed large quantities when sugar was added. Zoond (1926) also obtained negative results with various plant materials. Engel (1931*a*) determined gains of nitrogen and losses of carbon in soil with different plant materials and manures. The gains were often considerable, occasionally as high as 1 part of nitrogen per 8 parts of carbon lost as CO_2 (sheep dung in soil after 47 days), but were followed by even bigger losses (cf. Marr, 1910). The analytical error was stated, and shows that the gains are fully significant (possibility of a sampling error?). Olsen (1932) studied nitrogen fixation in decomposing leaves of different trees; the largest gain was found in beech leaves, where it amounted to 180 mgm. N per 100 gm. original material, or approximately 10 mgm. per gm. of organic matter lost during the decomposition. Olsen made the important observation that more nitrogen was fixed under (partially) anaerobic than under fully aerobic conditions, and that the fixation stopped as soon as nitrate began to accumulate in the medium (cf. Burk and Lineweaver, 1930). Clostridia, but not *Azotobacter*, were found in the material. Desai (1933) reported

[28] For instance, 3·71 mgm. N per 10 gm. soil with 0·1% straw, or 12·95 mgm. with 0·4% straw, corresponding to 325-370 mgm. N per gm. of straw. It is interesting to compare these results with those of Vandecaveye and Villanueva (1934), as stated above; both refer to soils from Washington, U.S.A.

big gains of nitrogen in Indian soils with addition of maize straw, even 47·5 mgm. N per gm. of straw that had previously undergone fermentation. Makrinow (1935) observed a rich development of *Azotobacter* in decomposing straw, where microscopic counts showed up to about 1000 mill. per gm. dry matter, accompanied by a two- to three-fold increase in nitrogen content (it is not clearly seen how much of this is due to disappearance of organic matter as CO_2). Turk (1936) found fixation of up to 60 p.p.m. nitrogen in soils with 2% lucerne material, and De and Pain (1936) reported small gains of nitrogen in soils with rice straw; in both instances, gains of nitrogen were stated to take place in the same soils without addition of organic matter, which again makes these claims appear doubtful. Vandecaveye and Allen (1935) found no gain of nitrogen in soil with addition of straw, plus sufficient NH_4NO_3 to give the straw a content of 2·5% N, although gains were stated to take place in control soil without straw; this result disagrees strongly with that of the previous cellulose experiments (Vandecaveye and Villanueva, 1934).

One cannot help being impressed with the lack of agreement between all these experimental results, and in many cases also with the lack of precise information on experimental methods and errors of analysis, as discussed above. True evidence of intensive nitrogen fixation in arid soils is not supplied by these data.

One thing, however, stands out clearly: celluloses and hemicelluloses as well as natural plant materials *can* serve as energy material for nitrogen fixation if partially transformed by other microorganisms into compounds assimilable by the nitrogen-fixers, and this process of fixation can be very economical, since it may reach 10–25 mgm. N per gm. of transformed organic matter (Pringsheim, 1909–10; Koch, 1910; Olsen, 1932), of which a not negligible fraction must have been used up by the organisms that provide food for the nitrogen-fixers; this may even be the case where *Azotobacter* is not involved. Whether the process can take place with an even higher efficiency under soil conditions appears uncertain, and on the whole the quantitative extent of the process is very variable and depends on a number of incompletely-known factors; for instance, practically nothing is known about the nature and quantity of the decomposition products that serve as energy material for the nitrogen-fixers under soil conditions. There is here an important scope for future investigations.

A number of experiments have been carried out in order to ascertain whether a significant nitrogen fixation takes place in wheat soils during decomposition of straw and related materials.

Experiment No. 1: *Oats-straw in soil under aerobic conditions.*—Ten soils from Table 2 were tested, all of them except No. 8 being wheat soils; No. 8 was again used as a control soil with addition of 0·2% $CaHPO_4$. The air-dry soil samples received additions of 1·5% finely ground oats-straw, and distilled water to approximately 60% of their water-holding capacity. The arrangement of the experiment was otherwise the same as in the previous series (incubation without addition of organic matter, and experiments with glucose). After incubation for 30 days at 28–30°C., samples were taken for nitrogen determination, and the rest of the soil was incubated further: where two parallels were run, the residues of soil from the two dishes were combined into one sample after 30 days. A special arrangement was made with soil No. 30; the first analysis was not made until after 75 days, and the remaining soil was then divided into three portions, which were further incubated with addition of: (1) nothing, (2) 0·003% Na_2MoO_4, and

(3) 0·02% Na_2HPO_4. Also soil No. 7 was after 30 days divided into two portions, one of which was given an addition of 0·5% $CaCO_3$. Tests for *Azotobacter* were made during or after incubation, either by plate counting or in some of the first experiments by planting of straw particles on plates of silica-gel with mannite. No bacteria other than *Azotobacter* made any conspicuous growth on either agar or silica-gel; a few fungi, which produced a certain amount of growth, were tested for nitrogen-fixation with a negative result (cf. Table 4). Tests for nitrate and ammonia were also made; nitrate was always found to disappear completely after 30 days, but small quantities of ammonia (2–4 p.p.m. NH_4–N) were sometimes found at the termination of the experiment.

The results are found in Table 14, in which the initial nitrogen contents have been calculated on the content of nitrogen in 100 parts of soil (based on determinations before and after incubation without organic matter, as in Table 10) plus 1·5 parts of straw (which in air-dry condition contained 0·202% N), converted to 100 parts of soil-straw-mixture. The *t*-test for the significance of the changes in nitrogen content may without any significant error be based on the sum of squares of deviations ($S(x-\bar{x})^2$) referring to nitrogen determinations on soil alone, since the figure represented by the nitrogen determinations on the straw is negligible in comparison herewith (0·74 per 15 gm. of straw).

The analytical data in Table 14 show that there is in no instance any significant gain of nitrogen, even in soils No. 8 and 10, where *Azotobacter* has multiplied strongly during incubation. On the contrary, we find, as in the experiments with glucose, in several instances a definite loss of nitrogen, most apparent after prolonged incubation (cf. Marr, 1910, and Engel, 1931*a*), and which bears no relation to the presence or absence of *Azotobacter*. The cause of this loss is obscure; in some cases it may be due to denitrification, which can sometimes take place at moderate degrees of moisture (Lemmermann and Wichers, 1914), but this cannot apply in examples like Nos. 10 and 30, where the losses took place *after* the disappearance of all nitrate during the first period of incubation. It is noteworthy that the fertile alkaline soil No. 30, even with addition of molybdenum or phosphate, shows a loss of nitrogen as in the glucose experiments (Table 11).

According to this preliminary experiment, oats-straw seems quite unsuitable for nitrogen fixation, although in soils of favourable reaction it may stimulate the development of *Azotobacter* to an extent far surpassing the numbers ever found under natural soil conditions. This negative result was not due to this particular batch of straw being in itself unsuitable as a material for nitrogen fixation, as was shown by a preliminary control experiment started before the soil experiments: 20·0 gm. of straw plus 1 gm. of $CaCO_3$ were moistened with a 0·1% solution of K_2HPO_4, inoculated with a suspension of garden soil, and incubated in a moderately moist condition for 11 months at 28–30°C. After incubation the sample had lost approximately one-third (6·3 gm.) of its weight of dry matter and gained approximately 10% (11·0 mgm.) nitrogen, corresponding to a fixation of about 1·7 mgm. N per gm. of organic matter lost. *Azotobacter* developed vigorously, and numbered about 11 mill. per gm. of dry matter (by plate counting) at the end of the experiment. No nitrate and only traces of ammonia were found. In order to get more exact data on the value of straw as an energy material for nitrogen fixation, two experiments were now carried out in a medium poorer in nitrogen than natural soils.

TABLE 14.

Nitrogen-fixation in Soils with Addition of 1·5% Oats-Straw.

Soil No., Treatment and Time of Incubation.	Total N, p.p.m., Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m., ($\bar{x}_2-\bar{x}_1$).	t.	P.
8. Initial..	467·0	11	804·0			
Inc. 30 d.	451·3	4	1118·8	*−15·7*	2·201	*0·05−0·02*
90 d.	468·2	5	1460·6	+1·2	0·175	0·9−0·8
	Azotobacter: Initial, 9 per gm. 7 and 18 d., abundant on silica-gel. 43 d., 0·94 mill. per gm. 89 d., 1·87 mill. per gm.					
10. Initial..	652·4	10	1038·1			
Inc. 30 d. (*a*) ..	650·0	3	546·0	−2·4	0·304	0·8−0·7
(*b*) ..	652·0	3	74·0	−0·4	0·060	1·0−0·9
70 d.	634·3	3	58·7	*−18·1*	2·741	*0·02−0·01*
120 d.	624·0	5	534·0	*−28·4*	8·609	*<0·01*
	Azotobacter: Initial, 20 per gm. 14 and 56 d., abundant on silica-gel. 107 d., 0·41 mill. per gm. Total count of bacteria: 1436±85·4 mill. *Azotobacter*-like: 8·9%.					
11. Initial..	654·6	14	2438·0			
Inc. 30 d. (*a*) ..	654·0	3	26·0	−0·6	0·074	1·0−0·9
(*b*) ..	643·5	4	961·0	−11·1	1·343	0·2−0·1
120 d.	655·0	5	826·0	+0·4	0·055	1·0−0·9
	Azotobacter: Present initially. 14 and 42 d., fair on silica-gel. 120 d., 1700 per gm.					
14. Initial..	669·5	12	2361·5			
Inc. 30 d. (*a*) ..	641·0	3	474·0	*−28·5*	2·990	*0·02−0·01*
(*b*) ..	655·3	3	32·7	−14·2	1·621	0·2−0·1
75 d.	657·0	3	216·0	−12·5	1·375	0·2−0·1
	Azotobacter: Present initially. 37 and 72 d., absent on dextrin-agar.					
15. Initial..	773·6	9	293·6			
Inc. 30 d. (*a*) ..	758·7	3	148·7	*−14·9*	2·812	*0·02−0·01*
(*b*) ..	760·3	3	484·7	−13·3	1·892	0·1−0·05
75 d.	754·5	4	323·0	*−19·1*	3·386	*<0·01*
	Azotobacter: Absent initially and after 37 and 72 days.					
7. Initial..	751·4	11	4101·6			
Inc. 30 d. (*a*) ..	739·3	3	184·7	−12·1	0·983	0·4−0·3
(*b*) ..	717·3	3	88·7	*−34·1*	2·802	*0·02−0·01*
60 d.	731·7	3	188·7	−19·7	1·600	0·2−0·1
plus 0·5% $CaCO_3$ (added after 30 days)	742·8	4	524·8	−8·6	0·782	0·5−0·4
	Azotobacter: Absent initially, after 30 days, and in soil +$CaCO_3$ after 40 days.					
1. Initial..	815·6	6	695·5			
Inc. 30 d.	812·0	3	6·0	−3·6	0·509	0·7−0·6
60 d.	832·1	3	418·7	+16·5	1·849	0·2−0·1
	Azotobacter: Absent initially and after 59 days.					

TABLE 14.—*Continued.*

6. Initial..	844·7	11	2528·8			
Inc. 30 d. (*a*) ..	834·8	4	2038·6	−9·9	0·719	0·5−0·4
(*b*) ..	843·3	3	1922·7	−1·4	0·112	1·0−0·9
75 d.	811·9	4	1979·9	*−32·8*	3·016	*<0·01*
	Azotobacter: Absent initially and after 20 days.					
30. Initial..	1086·7	10	1034·1			
Inc. 75 d.	1096·2	5	1991·2	+9·5	1·137	0·3−0·2
140 d.	1066·7	3	848·7	*−20·0*	2·322	*0·05−0·02*
Do. +0·003% Na_2MoO_4*	1063·8	4	1734·6	*−22·9*	2·549	*0·05−0·02*
Do. +0·02% Na_2HPO_4*	1063·8	4	978·8	*−22·9*	2·989	*0·02−0·01*
	Azotobacter: Present initially. 12 and 75 d., absent. 140 d.: Control soil 1600, +Na_2MoO_4 1100, +Na_2HPO_4, 1040 per gm.					
2. Initial..	1269·1	6	2004·6			
Inc. 30 d.	1270·0	3	1112·0	+0·9	0·060	1·0−0·9
60 d.	1248·3	3	242·7	−20·8	1·642	0·2−0·1
	Azotobacter: Absent initially and after 59 days.					

* Salts added in solution after 75 days.

Experiment 2*a*: *Oats-straw in "synthetic" soil under aerobic conditions.*—A kind of artificial soil was made up from 80% sand, 18·5% pure kaolin, 1·0% $CaCO_3$, 0·3% Fe_2O_3, and 0·2% $CaHPO_4$. Portions of 500 gm. of this mixture plus 10 gm. oats-straw were placed in large crystallizing dishes (lower dish 18·5 cm. wide and 4·5 cm. deep), and moistened with 60 c.c. of a solution containing 0·1% $MgSO_4$, 0·1% KCl, 0·05% NaCl, 0·05% $FeCl_3$, and 0·001% Na_2MoO_4; moreover, 5 c.c. of a 1:10 suspension of a soil rich in *Azotobacter* (No. 9, Table 2) were added as an inoculum to each dish. The soil-straw-mixture was in this way moistened to approximately 60% of its water-holding capacity. The dishes were incubated at 28–30°C., and nitrogen was determined at the start and periodically during 181 days; at intervals, plate counts of *Azotobacter* and direct counts of total bacteria were also carried out. The experiment was started in duplicate, but after 120 days the contents of the two dishes were combined into one. After one week numerous tiny brown glistening drops of mucus could be seen on the surface of the medium by means of a hand lens; microscopic examination showed these drops to be colonies of *Azotobacter*, practically free from other bacteria. The results are given in Table 15.

Both the plate counts and the direct counts show a luxuriant growth of *Azotobacter*, which is represented by numbers comparable with those in the glucose experiments. The numbers reach their maximum after 30–60 days, and then fall only slowly. The direct microscopic counts of *Azotobacter*-like organisms are only 2 to 5 times as high as the plate counts, and all through the experimental period they account for some 20–25% of the total bacterial numbers. If we consider the actual size of the cells, the *Azotobacter* account for a much larger proportion of the total mass of bacterial protoplasm; the rest of the population consisted chiefly of the small rods and cocci seen in normal soils, which hardly have an average volume of more than $1\mu^3$, or about one-fifth of the volume of a normal *Azotobacter*-cell. Compared with this both absolutely and relatively

TABLE 15.

Nitrogen-fixation in Sand-kaolin Mixture with 2·0% Oats-Straw.

Time of Incubation.	Total N, p.p.m., Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.
Initial	66·1	4	195·5			
60 d. (*a*)..	85·5	3	11·76	*+19·4*	3·954	*0·02—0·01*
(*b*)	86·1	3	8·66	*+20·0*	4·097	*<0·01*
120 d. (*a*)..	84·4	3	8·78	*+18·3*	3·748	*0·02—0·01*
(*b*)	79·8	3	27·13	*+13·7*	2·688	*0·05—0·02*
181 d. (*a*+*b*)	78·8	3	3·05	*+12·7*	2·639	*0·05—0·02*
Addition of 0·1% glucose after 181 d. inc. 4 days.						
Initial	78·8	3	3·05			
4 d. (*a*)	94·3	3	0·42	*+15·5*	20·35	*<0·01*
(*b*)	94·0	3	1·65	*+15·2*	17·17	*<0·01*

Number of Microorganisms:

Time of Incubation.	Direct Counts.			Plate Counts of *Azotobacter*, Mill. per gm.
	Total Bacteria. Mill. per gm.	*Azotobacter*-like. % of Total.	*Azotobacter*-like. Mill. per gm.	
10 d. (*a*)..	1262±75·7	16·9	213±25	
(*b*)	904±66·6	22·0	199±28	
15 d. (*a*)..	894±56·4	20·9	187±23	44·9
(*b*)	905±60·4	20·4	185±24	48·3
30 d. (*a*)..	930±59·4	24·6	229±31	70·8
(*b*)	750±56·7	23·9	179±25	67·6
60 d. (*a*)..	701±50·5	24·8	174±23	69·9
(*b*)	734±53·4	16·7	123±19	64·5
120 d. (*a*)..	640±40·2	14·2	91±13	51·4
(*b*)	480±31·3	10·4	50±9	32·8
181 d. (*a*+*b*)	273±23·2	13·9	38±9	21·9

abundant development of *Azotobacter*, the gain of nitrogen is only very moderate; after 60 days it amounts to about 20 p.p.m., and by further incubation it not only does not increase, but actually declines a little, as in some of the experiments in soil (Table 14). If, as before, we assume that 1000 mill. *Azotobacter*-cells represent 0·1 mgm. cell-nitrogen, we find after 60 days 12 and 17 p.p.m. nitrogen represented by the 123 and 174 mill. cells per gm. by direct counting, or 60 and 85% of all the nitrogen fixed. When it is remembered that large numbers of cells must have arisen and died before this time, it seems clear that the gain of nitrogen is due to simple synthesis of cell material. After this time it seems that the cells have continued to exist in a resting condition without fixing more nitrogen.

When the experiment was terminated, the medium contained no nitrate and only a minute quantity (1·0 p.p.m.) of NH_4–N. A control experiment was now carried out: a portion of the air-dry material was re-moistened to its original

moisture content, given an extra addition of 0·1% glucose, and incubated for 4 days at 28–30°C. Total nitrogen was then determined. This addition of a small quantity of available energy material resulted in a vigorous nitrogen fixation, corresponding to 15–16 mgm. N per gm. of glucose, and similar to the yield in a vigorously fixing pure culture. This shows plainly that the inactivity of *Azotobacter* after the 60-day period was not due to any active inhibitory factor, but presumably to a failing supply of available organic nutrients.

While this experiment proves that straw can serve as energy material for nitrogen fixation under conditions favourable for the growth of *Azotobacter*, it also shows that the gain is comparatively small and only corresponds to about 1·0 mgm. N per gm. of straw present—a quantity which would indeed have been difficult to detect in a soil of normal nitrogen content with 1·5% straw; also the small quantities of nitrate and ammonia normally present in the soil would automatically tend to counteract this slight fixation.

As shown by Olsen (1932), nitrogen fixation on the basis of complex plant materials may be more vigorous under partially anaerobic[27] than under fully aerobic conditions. An experiment to test this point was therefore carried out with the straw.

Experiment 2*b*: *Oats-straw in water-saturated medium.*—For this experiment a pure sand medium was used, with addition of 1·0% $CaCO_3$ and 0·2% $CaHPO_4$. Portions of 800 gm. sand plus 12 gm. straw were moistened with 195 c.c. nutrient solution (0·1% $MgSO_4$, 0·1% KCl, 0·1% $FeCl_3$, 0·001% Na_2MoO_4) and 5 c.c. of the same soil suspension as the previous experiment. This saturated the sand-straw-mixture completely, without forming an actual layer of liquid over the surface. Duplicate dishes, as in Experiment 2*a*, were incubated at 28–30°C., and after 100 days combined into one sample. The results of this experiment are seen in Table 16.

The development of *Azotobacter* is here only moderate in comparison with the previous experiment, although this organism is constantly present, in numbers of 1 to 3 mill. per gm. in the period from 28–60 days, during which time the nitrogen fixation was most intense. The direct microscopy certainly showed presence of *Azotobacter*-like cells, but they were too few to admit of any reliable counting, especially in the later periods. The nitrogen fixation is far more vigorous than under aerobic conditions; during the first 4 weeks it is only moderate, but during the next 32 days approximately 30 p.p.m. nitrogen are fixed; the rate of fixation then becomes slower, and at the end of the experiment the total gain (93 p.p.m.) corresponds to a fixation of approximately 6 mgm. N per gm. of straw originally supplied—a figure very similar to the maximal fixation found by Hutchinson (1918) with straw in soil-sand mixture. This stronger fixation might be due, as Olsen (1932) suggests, to a production of larger amounts of organic by-products suitable as nutrients for the nitrogen-fixers. Whether *Azotobacter* or other organisms were chiefly responsible for the fixation is a more difficult question. There can be little doubt, however, that the activity of *Azotobacter* may account for the gains during the first two months of the experiment, although their numbers were much lower than in the previous experiment under aerobic conditions. It is very likely that the higher water-content would favour the development of protozoa (numerous active ciliates and flagellates could actually

[27] The "anaerobic" conditions in Olsen's experiments were produced merely by supersaturation of the leaf material with water. Aerobic organisms could thus still have displayed some activity on the surface of the medium.

TABLE 16.

Nitrogen-fixation in Water-saturated Sand with 1·5% Oats-straw.

Time of Incubation.	Total N, p.p.m., Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	*Azotobacter* Plate Count. Millions per gm.
Initial ..	50·5	3	3·71				
28 d. (*a*)	67·3	3	0·67	*16·8*	19·66	*<0·01*	3·05
(*b*)	60·0	3	0·86	*9·5*	10·79	*<0·01*	2·85
60 d. (*a*)..	95·9	3	0·05	*45·4*	*	—	1·03
(*b*)	88·9	3	19·23	*38·4*	—	—	2·24
100 d. (*a*)..	112·3	3	2·11	*61·8*	—	—	0·56
(*b*)	100·1	3	2·09	*49·6*	—	—	0·55
116 d. (*a*+*b*)					—	—	0·41
150 d. ..	123·6	4	8·84	*73·1*	—	—	0·047
179 d. ..					—	—	0·012
200 d. ..	138·6	4	5·03	*88·1*	—	—	0·010
250 d. ..	143·8	3	4·03	*93·3*	—	—	0·006

Direct counts, millions per gram:

Time.	Total Bacteria.	*Azotobacter*-like Org., % of Total.	
28 d. (*a*)..	310±25·1	8·5	–
(*b*)	480±46·3	5·9	
60 d. (*a*)..	932±44·7	4·7	Typical clostridia were seen only sporadically (less than 0·1% of total). Numerous short, plump, vibrio-like bacteria, and some long, slender rods with oval terminal spores, closely resembling anaerobic cellulose-decomposing bacteria.
(*b*)	910±48·5	2·1	
100 d. (*a*)..	764±36·7	2·0	
(*b*)	638±36·4	1·7	
150 d. ..	1485±72·7	1·4	
200 d. ..	591±35·5	0·5	

* In this and subsequent cases the values of *t* are much higher than after 28 days, and the calculation therefore superfluous.

be seen by direct microscopic examination of the fluid from the sand), which by feeding on the *Azotobacter*-cells would increase their death-rate and thereby prevent them from accumulating as resting cells in such numbers as observed under aerobic conditions, while still permitting the renewed production of young and active *Azotobacter*-cells, as suggested by Cutler and Bal (1926). The fixation of 45 p.p.m. nitrogen in the first 60 days would require a production of 450 mill. cells per gm., or an average daily production of 7·5 mill. new cells per gm. (assuming, as before, that 1000 mill. cells equal 0·1 mgm. N)—a figure not incompatible with the numbers of 1 to 3 mill. *Azotobacter* found by plate counting. The actual numbers, although they could not be counted with any accuracy, must certainly have been somewhat higher; it must be remembered that we know nothing about the rates of reproduction and death of *Azotobacter*-cells in the soil, but there is nothing obviously wrong in the assumption that a stationary population of some 2–3 mill. *Azotobacter* could have renewed itself 3 times during 24 hours, thereby producing a total of 6–9 mill. new cells per gm., which in the present case may safely be assumed to have taken all their nitrogen from the atmosphere, since no trace of nitrate or ammonia could ever be detected in the medium. (It should not be forgotten, however, that the growth of *Azotobacter* must have taken place in the surface layers of the medium; in the depth the conditions were

completely anaerobic, as shown by the clearly visible formation of iron sulphide.) During the last 100 days of the experiment this explanation seems definitely to break down. The gain of nitrogen in this period amounts to 20 p.p.m., which would require a total production of some 200 mill. *Azotobacter*-cells, or an average daily formation of 2 mill. new cells per gm.—a rate of reproduction which is difficult to reconcile with the relatively low numbers (6,000 to 47,000) shown by the counts; and even these numbers fall steadily throughout the period. Unless we make the assumption (for which there is no positive evidence) that the relation between nitrogen fixation and cell production in *Azotobacter* has here been quite different from that in pure cultures, where the fixation is "growth-bound", we cannot escape the conclusion that in this experiment other organisms must, at least in the later stages, have contributed to the fixation. It does not appear very likely that these other organisms should be *Cl. pasteurianum* and related types, since vegetative clostridia were hardly ever visible in the direct counts, in contrast to the experiments with glucose (Table 12), where they dominated the picture, while carrying out only a moderate fixation. But in view of the much longer duration of the present experiments, no very definite conclusion can be drawn. It may also be that we have here a case of "non-specific" nitrogen fixation due to other organisms producing nascent hydrogen in their metabolism; this possibility is worthy of further investigation (cf. Clausen's (1931) remarkable findings on nitrogen fixation by anaerobic cellulose-decomposing bacteria).

While all these considerations should not be taken for more than an attempt to explain the mechanism of nitrogen fixation, the two experiments have shown conclusively that straw can indeed serve as energy material for an appreciable fixation of nitrogen, but more so under semi-anaerobic than under aerobic conditions—a result in sharp contrast to the frequently expressed views concerning a particularly intensive nitrogen fixation under arid soil conditions, but in perfect agreement with the findings of Olsen (1932); indeed, the difference is much more pronounced here than in Olsen's experiments with leaf material.[28] We shall now see what happens in natural soil under conditions of high moisture and addition of straw.

Experiment 3*a*: *Oats-straw in water-saturated soil.*—This was carried out with a typical wheat soil of moderately acid reaction, with and without addition of calcium carbonate. The soil was a mixture of equal parts of soils No. 14 and 15 (Table 2), which had been washed free from nitrate and then air-dried. Duplicate portions of 250 gm. air-dry soil were given additions of 1·0% ground oats-straw, ± 1·0% $CaCO_3$, and 0·005% Na_2HPO_4, and were moistened with 46 c.c. H_2O plus 1 c.c. of a 1:10 suspension of soil No. 21 after incubation anaerobically with glucose (Table 12); this inoculum served to introduce both *Azotobacter* and *Cl. pasteurianum.* The addition of moisture was sufficient to saturate the soil completely, so that it formed a compact plaque, about 12 mm. deep, in the usual big Petri dishes used for incubation of soils. The samples were incubated at 28–30°C. for 120 days, and periodical nitrogen determinations, direct counts, and plate counts of *Azotobacter* were carried out; after 78 days the two parallel dishes were combined into one. After 4 days' incubation the dishes with addition of $CaCO_3$ showed on their surface numerous small drop-like bacterial colonies which after 6–7 days turned dark and microscopically revealed themselves as *Azotobacter-*

[28] In this connection it is also interesting to note that Richards (1917) found nitrogen fixation in dung with extra addition of water, but not in material of normal moisture content.

colonies; the picture was similar to that of the soil plaques with addition of starch. When the soils had been disturbed after the first sampling (14 days) this growth did not reappear. The dishes without $CaCO_3$ remained permanently free from macroscopically visible growth of *Azotobacter*, but showed quite a conspicuous growth of black fungal mycelium on the surface. The experimental data are seen in Table 17.

TABLE 17.

Nitrogen-fixation in Water-saturated Soil (Mixture of Nos. 14 and 15) plus 1·0% Oats-straw.

Time of Incubation.	Total N, p.p.m., Mean ($\bar{x}$). (Catalyst: Se).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m., ($\bar{x}_2-\bar{x}_1$).	t	P.	*Azotobacter* Plate Count. 1,000 per gram.
I. $-CaCO_3$. pH initial: 5·6. pH final: 6·0.							
Initial ..	680·3	4	224·76				0·190
70 d. (*a*)..	688·5	2	14·05	+8·2	1·225	0·3—0·2	
(*b*)	681·7	3	10·67	+1·4	0·267	0·8—0·7	
90 d. (*a*+*b*)							1·40
120 d. (*a*+*b*)	684·3	4	5·56	+4·0	0·913	0·4—0·3	4·40
II. +1·0% $CaCO_3$. pH final: 7·7.							
Initial ..	681·3	4	104·76				0·190
14 d. (*a*)..	666·7	3	98·67	*−14·6*	2·997	*0·05—0·02*	1320·0
(*b*)	680·0	3	96·00	*−1·3*	0·269	0·8—0·7	1780·0
70 d. (*a*)..	699·7	3	180·67	*+18·4*	3·189	*0·05—0·02*	1174·0
(*b*)	692·3	3	4·67	*+11·0*	3·078	*0·05—0·02*	2075·0
90 d. (*a*+*b*)							3370·0
120 d. (*a*+*b*)	694·0	4	54·00	*+12·7*	3·490	*0·02—0·01*	3840·0

Direct Counts.	Total Bacteria, Mill. per gm.	*Azotobacter*-like Organisms. % of Total.	*Azotobacter*-like Organisms. Mill. per gm.	
$-CaCO_3$, 70 d. (*a*) ..	753±62·9	1·0	(8)	
(*b*) ..	421±40·7	2·3	(10)	Vegetative clostridia were seen sporadically only (less than 1% of total).
$+CaCO_3$, 70 d. (*a*) ..	548±49·3	0·7	(4)	
(*b*)	668±58·7	2·8	(19)	
120 d. ..	636±50·8	3·8	(22)	

In soil without lime the reaction becomes slightly less acid during incubation, but it still remains unfavourable for the growth of *Azotobacter*. In spite of this, *Azotobacter* has multiplied to a certain extent after 90–120 days, when it is present in numbers rarely found under natural soil conditions, even at favourable reaction. About two-thirds of the colonies counted after 120 days were *Az. vinelandii*—the only occasion when this species was encountered.[29] Although a strain isolated herefrom showed vigorous nitrogen-fixation in pure culture

[29] The colonies were rather smaller and less compact than those of *Az. chroococcum*, and remained pure white on dextrine agar. On agar with glucose, saccharose or mannite the organism grew better and produced the typical greenish-yellow soluble pigment. Morphologically the organism was similar to *Az. chroococcum*, but showed an active motility in young cultures.

(Table 4), the soil shows no gain of nitrogen that even begins to approach significance. In the dishes with addition of lime the macroscopic growth of *Azotobacter* is reflected in the very large numbers found by plate counting after 14 days and for the rest of the experimental period, during which they tend to rise rather than to fall. The nitrogen-figures show no gain during the first 14 days, when the first explosive development of *Azotobacter* took place; actually one of the dishes shows a loss which appears significant. After 70 days the gain becomes only just significant, and remains so after 120 days, when it corresponds to a fixation of about 1·3 mgm. N per gm. of straw added to the soil. The final gain of 12·7 p.p.m. nitrogen would only require a total production of some 130 mill. *Azotobacter*-cells per gm. of soil, a figure that might well be expected where the plate counts show numbers of about 1 to 4 mill. per gm. The direct counts towards the end of the experiment are relatively low and not much influenced by the lime. The *Azotobacter*-like organisms are too few to admit of any reliable counting, and the extremely sparse representation of clostridia (which never showed a typical morphological appearance) does not suggest that they had taken any part in the fixation. It may here be mentioned that other observations on soil plaques of the same depth and water saturation as used in this experiment, but with addition of glucose, showed a vigorous growth of clostridia;[30] their absence in this experiment was thus not due to a too high oxygen-tension.

Experiment 3*b*: *Oats-straw in water-saturated soil.*—This was a smaller experiment, carried out in connection with the previous one, on soils No. 10 and 11 after incubation for 30 days with addition of 1·5% straw, which did not result in any fixation (Exp. 1, Table 13). Equal parts of samples *a* and *b* (75 gm. of No. 10, 40 gm. of No. 11) were moistened to complete saturation and incubated at 28–30°C. in small glass cylinders with lids that did not fit air-tightly. Nitrogen was determined in No. 10 after 62 and 90 days, in No. 11 only after 35 days; at the same time plate counts of *Azotobacter* were carried out. Table 18 gives the results.

TABLE 18.

Nitrogen-fixation in Water-saturated Soils with 1·5% Oats-straw.

Soil No. and Time of Incubation.	Total No. p.p.m., Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	*Azotobacter* 1,000 per gm.
10. Initial ..	651·0	6	626·0	—	—	—	—
Inc. 62 d.	667·3	3	28·7	*+16·3*	2·442	*0·05—0·02*	321·0
90 d.	654·7	3	88·7	+3·7	0·518	0·7—0·6	630·0
11. Initial ..	648·0	7	1176·0	—	—	—	0·54
Inc. 35 d.	637·0	3	122·0	−11·0	1·249	0·3—0·2	4·70

Soil No. 10 shows, after 62 days, a barely significant gain of nitrogen, corresponding to about 1·1 mgm. N per gm. of straw originally introduced, but after 90 days this has become non-significant, although the numbers of *Azotobacter* have increased. Small quantities of nitrate and ammonia could be detected at this

[30] The starch plaques (Table 12) also frequently showed gas bubbles and smell of butyric acid.

stage. In soil No. 11 the multiplication of *Azotobacter* is only slight, and no gain of nitrogen has taken place; no nitrate or ammonia was present.

These experiments show that even a long-protracted decomposition of oats-straw in water-saturated soil will even at the best (soil with addition of lime and phosphate) result in only a very moderate fixation of nitrogen not exceeding 2 mgm. N per gm. of straw introduced, and this is associated with a vigorous multiplication of *Azotobacter*. Another experiment was now set up with wheat straw, which represents a more important source of organic matter in the wheat soils.

Experiment 4: *Wheat straw in soil of high and low moisture.*—A faintly acid soil (pH 6·3) of very low humus content (equal parts of soils No. 31 and 33, Table 2) was used. Portions of 500 gm. air-dry soil received additions of 5·0 gm. finely ground wheat straw, 50 c.c. of a solution containing 0·15% K_2HPO_4 and 0·015% Na_2MoO_4, and 10 c.c. of a 1:20 suspension of soil No. 44 to ensure the presence of *Azotobacter*. The soil portions were placed in 10 cm. wide glass jars covered with Petri dishes, and were given the following extra additions: Jars 1–2: Nothing; Jars 3–4: 5·0 gm. $CaCO_3$; Jars 5–6: 30·0 c.c. H_2O; Jars 7–8: 30·0 c.c. H_2O + 5·0 gm. $CaCO_3$.

The extra addition of water made the soil completely saturated. The jars were incubated at 28–30°C., and nitrogen-determinations and plate counts of *Azotobacter* were carried out on the original material as well as periodically during 3 months of incubation. (The initial nitrogen-determinations on soil with and without $CaCO_3$ agreed within the analytical error, which was rather large in the former case; the average was therefore taken to represent the initial nitrogen content.) In the jars with high moisture, and particularly in those with lime (Nos. 7–8), growth of *Azotobacter* became visible as large slimy colonies on the surface after 3–4 days (Pl. i, fig. 6). The rest of the data are seen in Table 19.

TABLE 19.

Nitrogen-fixation in Soil of High and Low Moisture Content, with addition of Wheat-straw.

Treatment and Time of Analysis.	Total N, p.p.m., Mean ($\bar{x}$). (Catalyst : Se.)	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	*Azotobacter* 1,000 per gm.
Initial :							
Soil−$CaCO_3$	223·4	4	14·94	—	—	—	
Soil+$CaCO_3$	227·1	6	215·45	—	—	—	
Average ..	225·6	10	265·44	—	—	—	0·018
Soil−$CaCO_3$, low moisture (10·8% H_2O).							
7 d. (*a*) ..	—	—	—	—	—	—	(>100)
(*b*) ..	—	—	—	—	—	—	(>100)
14 d. (*a*) ..	—	—	—	—	—	—	862
(*b*) ..	—	—	—	—	—	—	964
28 d. (*a*) ..	227·1	3	20·18	+1·5	0·447	0·7−0·6	1,240
(*b*) ..	226·3	2	6·48	+0·7	0·248	0·9−0·8	934
56 d. (*a*) ..	225·2	3	6·72	−0·4	0·122	1·0−0·9	460
(*b*) ..	218·4	3	2·66	−7·2	2·216	*0·05−0·02*	345
90 d. (*a*) ..	221·1	3	5·82	−4·5	1·375	0·2−0·1	176
(*b*) ..	220·7	3	21·25	−4·9	1·442	0·2−0·1	60

TABLE 19—*Continued.*

Soil + $CaCO_3$, low moisture (10·8% H_2O).

7 d.	(*a*) ..	—	—	—	—	—	—	1,500
	(*b*) ..	—	—	—	—	—	—	1,830
14 d.	(*a*) ..	—	—	—	—	—	—	5,820
	(*b*) ..	—	—	—	—	—	—	5,380
28 d.	(*a*) ..	227·1	3	11·65	+1·5	0·454	0·7—0·6	2,711
	(*b*) ..	223·1	3	1·46	−2·5	0·771	0·5—0·4	2,018
56 d.	(*a*) ..	225·7	3	6·58	+0·1	0·031	1·0—0·9	1,710
	(*b*) ..	225·9	3	46·89	+0·3	0·086	1·0—0·9	846
90 d.	(*a*) ..	221·7	3	11·53	−3·9	1·180	0·3—0·2	1,599
	(*b*) ..	221·7	3	11·53	−3·9	1·180	0·3—0·2	868

Soil − $CaCO_3$. high moisture (15·4% H_2O).

7 d.	(*a*) ..	—	—	—	—	—	—	1,017
	(*b*) ..	—	—	—	—	—	—	1,658
14 d.	(*a*) ..	—	—	—	—	—	—	1,563
	(*b*) ..	—	—	—	—	—	—	3,625
28 d.	(*a*) ..	233·2	3	0·33	*+7·6*	2·351	*0·05—0·02*	1,840
	(*b*) ..	236·2	3	2·81	*+10·6*	3·261	*<0·01*	6,540
56 d.	(*a*) ..	233·0	3	2·47	*+7·4*	2·272	*0·05—0·02*	3,390
	(*b*) ..	243·1	3	11·76	*+17·5*	5·296	*<0·01*	5,330
90 d.	(*a*) ..	236·8	3	0·89	*+11·2*	3·458	*<0·01*	5,697
	(*b*) ..	251·8	3	7·39	*+26·2*	7·850	*<0·01*	9,444

Soil + $CaCO_3$, high moisture (15·4% H_2O).

7 d.	(*a*) ..	—	—	—	—	—	—	5,650
	(*b*) ..	—	—	—	—	—	—	4,880
14 d.	(*a*) ..	—	—	—	—	—	—	7,470
	(*b*) ..	—	—	—	—	—	—	6,540
28 d.	(*a*) ..	245·1	3	13·81	*+19·5*	5·879	*<0·01*	9,504
	(*b*) ..	242·1	3	6·80	*+16·5*	5·038	*<0·01*	10,170
56 d.	(*a*) ..	244·4	3	14·64	*+18·8*	5·660	*<0·01*	7,340
	(*b*) ..	239·6	2	2·64	*+14·0*	3·491	*<0·01*	7,130
90 d.	(*a*) ..	258·1	3	0·99	*+32·5*	10·03	*<0·01*	4,420
	(*b*) ..	252·9	3	7·05	*+27·3*	8·333	*<0·01*	5,414

Soil + $CaCO_3$, low moisture, after 90 d., with extra addition of 0·5% Ca-acetate.

Initial	..	221·7	6	23·06	—	—		—
7 d.	..	240·7	3	6·59	*+19·0*	13·06	*<0·01*	11,3500

pH of soil initially: 6·3. pH values after 90 days:

− $CaCO_3$, low moisture	(*a*) 6·1	+ $CaCO_3$, low moisture	(*a*) 7·8
	(*b*) 6·2		(*b*) 7·8
high moisture	(*a*) 6·8	high moisture	(*a*) 7·9
	(*b*) 6·9		(*b*) 8·0

The soil of low moisture-content shows, both with and without addition of lime, a very strong multiplication of *Azotobacter*, which reaches its maximum after 2–4 weeks and then recedes somewhat; this is most pronounced in the soil without lime, where the numbers also, as might be expected, are considerably

lower than where lime is added. In both series, however, there is absolutely no indication of any gain of nitrogen; on the contrary, a small loss of nitrogen seems to have taken place in one of the jars in the series without lime after 56 days. A very different picture is seen at high degree of moisture. The numbers of *Azotobacter* are considerably higher than in the previous series; in soil with lime they reach a maximum of about 10 mill. per gm. after 4 weeks and then fall only slowly, but in the soil without lime they continue to rise steadily throughout the whole period; this phenomenon is reflected in the circumstance that the originally faintly acid soil in this series had become almost neutral at the end of the experiment, as shown at the bottom of the table (cf. Olsen (1932) on beech and oak leaves under anaerobic conditions). The nitrogen-figures show significant but somewhat irregular gains of nitrogen. In the series with lime the increase is rapid at first, seems to stop in the period from 38 to 56 days, and then begins again. In the unlimed soil the gain of nitrogen takes place less rapidly, but in one of the jars it reaches the same level as in the soil with lime after 90 days; the disagreement between these two parallel jars corresponds to a similar difference in the numbers of *Azotobacter*, which are consistently higher in jar *b*, where the stronger fixation has taken place.

These results are quite in agreement with those found in the previous experiments with oats-straw: absolutely no nitrogen fixation under aerobic conditions, even where the conditions for the growth of *Azotobacter* are optimal, and where these organisms actually multiply to the extent of several millions per gm. of soil—and under semi-anaerobic conditions after incubation for 3 months only a moderately strong fixation, corresponding to 2·5–3·0 mgm. N per gm. of straw originally added. This gain is apparently due to *Azotobacter*, which here flourishes even more strongly than under fully aerobic conditions. This last phenomenon is rather surprising in view of the essentially aerobic character of *Azotobacter*; the best explanation would seem to be that under semi-anaerobic conditions larger quantities of organic matter become available as carbonaceous food for *Azotobacter*, through the decomposition of the straw cellulose and hemicelluloses, which are not directly available to *Azotobacter*. Now it is well known that fungi, which play a very important part in the decomposition of cellulose in soil under aerobic conditions, transform the cellulose almost quantitatively into mycelial substance, carbon dioxide, and water (Waksman, 1932), and in pure cultures of most aerobic cellulose-decomposing bacteria there is little or no accumulation of soluble organic compounds, unless growth is suspended by high temperature or by exclusion of the oxygen and the cellulose-decomposing enzymes thus enabled to act independently (Kalnins, 1930). On the other hand, anaerobic cellulose-decomposing bacteria produce large quantities of organic acids which are excellent sources of energy for *Azotobacter* (Waksman (1932) quotes data showing 50–66% of the cellulose being converted into fatty acids by the organisms of Omeliansky, and 75% of the cellulose-carbon into acetic acid and ethyl alcohol by the *Clostridium thermocellum* Viljoen et al.), and the same thing may apply to the decomposition of hemicelluloses. That the lack of such decomposition products is the reason why no fixation took place under aerobic conditions was strongly suggested by a control experiment with soil from the third series (low moisture, addition of $CaCO_3$) of Experiment 4 after incubation for 90 days. A mixture of equal parts of soil from jars *a* and *b* was given an addition of 0·5% calcium acetate and 12% H_2O, and incubated for 7 days at 28–30°C.; nitrogen determination and plate count of *Azotobacter* were then carried out. The data

are included in Table 19. As in the similar experiment with addition of glucose to sand-kaolin-mixture in Experiment 2*a*, the provision of a small quantity of directly available energy material immediately resulted in a vigorous nitrogen fixation, which corresponds to very nearly 5 mgm. N per gm. of acetic acid, and which is accompanied by a luxuriant growth of *Azotobacter*; the production of approximately 110 mill. *Azotobacter*-cells per gm. of soil shown by the plate count would alone, provided the cells were of normal average size, account for a fixation of 11 p.p.m. N, or more than half the quantity actually fixed.

Another experiment shows the importance of a sufficient supply of soluble decomposition products even more strikingly.

Experiment No. 5: *Filter paper in soil under aerobic conditions.*—This experiment was originally planned in the hope of obtaining quantitative data on the correlation between numbers of *Azotobacter*, fixation of nitrogen, and decomposition of cellulose. The soil used here was similar to that of the previous experiment—a light sand soil very poor in humus and of faintly acid reaction (No. 32, Table 2). Duplicate portions of 830 gm. air-dry soil received additions of 1·0% finely ground filter paper, 1·0% $CaCO_3$, and 12·5% of a nutrient solution containing 0·4% K_2HPO_4 and 0·04% Na_2MoO_4. Incubation took place in the same large glass dishes as in Experiment No. 2. A special inoculum was prepared in order to ensure the presence of both nitrogen-fixing and actively cellulose-decomposing bacteria able to exist in symbiosis with each other: 3 gm. of strips of filter paper and 2 gm. of $CaCO_3$ were covered with 40 c.c. of a nitrogen-free nutrient solution in a deep Petri dish, infected with soil No. 44, and incubated at 28–30°C. After a few weeks the paper appeared visibly decayed, and colonies of *Azotobacter* started to grow on the pieces of paper that reached the surface; an emulsion of this material was used as inoculum, at the rate of 0·5 c.c. per 100 gm. soil. The results are seen in Table 20.

The paper showed no visible attack by microorganisms, and quantitative determination of the cellulose was not continued. The numbers of *Azotobacter* declined steadily during two months of incubation and no significant gain of nitrogen took place. The experiment was discontinued after 60 days, and control experiments were set up with duplicate portions of 60 gm. air-dry soil re-moistened to their previous degree of moisture and with further addition of: (*a*) 0·2% glucose; (*b*) 0·5% calcium lactate; (*c*) 0·5% calcium acetate.

The samples with glucose and lactate were incubated for 7 days and those with acetate for 8 days at 28–30°C., when nitrogen was determined and direct and plate counts of *Azotobacter* carried out. As shown in Table 20, these additions resulted in a vigorous nitrogen fixation, which corresponds to very nearly 14 mgm. N per gm. of glucose and 5·3–6·5 mgm. per gm. of salt of the two organic acids (or 7·3–8·2 mgm. per gm. of acid). As in the control experiments with glucose and Ca-acetate belonging to Experiments No. 2*a* and 4, this is comparable with the yield in a vigorously fixing pure culture of *Azotobacter*; particularly the acetate seems here to have been utilized very efficiently (Mockeridge (1915) and Gainey (1928) found only 2·6–3·8 mgm. N fixed by *Azotobacter*, per gm. of acetic acid consumed, whereas Hunter (1923) briefly mentions a fixation of 8 mgm. N per gm. of potassium acetate; it should be noted that no molybdenum was added to the media in any of these experiments). The fixation was bound up with an enormous development of *Azotobacter*, which, especially in the soil with lactate, rose to surprising numbers. The microscopic counts showed that the numbers of *Azotobacter*-like organisms were only about

3 times as high as the plate counts (as in Exp. 2*a* in this series, and the glucose-experiments in Table 11 where the plate counts were high). The *Azotobacter*-like cells in this experiment appeared rather small, and this was particularly the case in soil plus lactate (cf. Winogradsky, 1926), where they were little more than 1μ in diameter, but intensely staining (Pl. i, fig. 5). Since the actual size of the living cells cannot be ascertained, we cannot calculate the amount of cell nitrogen with any reasonable accuracy.

TABLE 20.

Nitrogen-fixation in Sand Soil with Cellulose, and with Low Concentrations of Glucose or Salts of Organic Acids.

Time of Incubation.	Total N. p.p.m., Mean ($\bar{x}$). (Catalyst: Se.)	n+1.	$S(x-\bar{x})^2$.	Gain of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	*Azotobacter* Plate Count Millions per gm.
I. Soil No. 32, with 1% $CaCO_3$ and 1% filter paper.							
Initial ..	246·0	4	58·0				0·127
18 d. (*a*) ..							0·081
30 d. (*a*) ..	249·0	3	26·0	3·0	0·958	0·4—0·3	0·067
(*b*) ..	249·7	3	34·67	3·7	1·125	0·4—0·3	0·071
60 d. (*a*) ..	252·3	3	18·67	6·3	1·916	0·2—0·1	0·041
(*b*) ..	248·7	3	2·67	2·7	1·015	0·4—0·3	0·036
II. After 60 days, addition of (*a*) 0·2% glucose, (*b*) 0·5% Ca-lactate, (*c*) 0·5% Ca-acetate.							
Initial ..	250·5	6	41·5				
Glucose:							
Inc. 7 d. (*a*)	279·0	3	38·0	*28·5*	11·96	<*0·01*	78·1
(*b*)	278·3	3	33·67	*27·8*	12·00	<*0·01*	75·9
Lactate:							
7 d. (*a*) ..	283·3	3	24·67	*32·8*	15·09	<*0·01*	214·0
(*b*) ..	277·3	3	24·67	*26·8*	12·33	<*0·01*	232·0
Acetate:							
8 d. (*a*) ..	277·0	3	6·00	*26·5*	15·06	<*0·01*	91·2
(*b*) ..	277·0	3	8·00	*26·5*	14·09	<*0·01*	81·6

Direct Counts.	Total Bacteria. Mill. per gm.	*Azotobacter*-like Org. Mill. per gm.	Average Diameter of *Azotobacter*-like Cells (μ).
Glucose 7 d. (*a*) ..	1133±71·4	212±26·2	1·29
(*b*) ..	958±58·1	199±22·5	
Lactate 7 d. (*a*) ..	1615±87·9	603±44·8	1·04
(*b*) ..	1488±76·6	566±39·9	
Acetate 8 d. (*a*) ..	893±57·1	250±27·3	1·11
(*b*) ..	750±53·3	237±26·5	

This experiment shows plainly that even where the general soil conditions for the growth of *Azotobacter* are excellent (temperature, reaction, aeration, supply of phosphate and molybdenum), and where we have supplied a potential source of energy (cellulose) and organisms capable of converting this into food material for *Azotobacter* in solution cultures, there may still not be a sufficient production of available organic matter to induce a measurable fixation of nitrogen (cf. Koch, 1910); it seems that the required cellulose-decomposing bacteria do not find

suitable conditions for development in moderately moist soil, or at least fail to produce soluble organic compounds from the cellulose (cf. the important observation of Kalnins (1930) that aerobic cellulose-decomposing bacteria produce more reducing sugars when deprived of oxygen). In Experiments No. 2–4 there was always, except in the acid soil in Exp. 3*a*, a rapid multiplication of *Azotobacter* after the addition of straw, which thus seems to contain certain substances directly available to *Azotobacter* (cf. Dvorak, cit. after Fulmer (1917) and Waksman (1932)). According to Waksman and Hutchings (1937), *Azotobacter* can utilize the water-soluble constituents of oats-straw without, however, fixing any nitrogen, and Hunter (1923) found nitrogen fixation in glucose solution slightly stimulated by addition of straw. Some experiments were carried out in order to ascertain the value of the water-soluble constituents as well as the insoluble residue of straw as energy materials for nitrogen fixation.

Experiment No. 6: *Water-extract of wheat straw as a medium for* Azotobacter.—60 gm. of finely-ground wheat straw were heated for 1 hour in the steamer with 600 c.c. H_2O, filtered, and washed on the filter with distilled water until the filtrate had been made up to 600 c.c. The extracted straw was further washed repeatedly with distilled water and then dried. The extract was given an addition of 0·02% K_2HPO_4, 0·01% $FeCl_3$, 0·005% Na_2MoO_4, and 0·4% $CaCO_3$, distributed in portions of 50 c.c. in 300 c.c. Erlenmeyer flasks, and sterilized. Before the addition of the salts the extract was found to contain 0·125% dry matter with 9% ash, i.e. 50 c.c. of medium contains 0·570 gm. dry organic matter. The flasks were inoculated with *Az. vinelandii* and *Az. chroococcum* (strain 34), and cultures as well as controls incubated at 28–30°C. The results are given in Table 21.

TABLE 21.

Nitrogen-fixation by Azotobacter *in Water-extract of Wheat-straw.*

Culture.	Incubation Days.	Total N per Culture, Mgm.	Gain of Nitrogen, Mgm.	
			Per Culture.	Per gm. of Org. Matter Present.
Control initially (*a*) ..	0	2·60 } 2·66	—	—
(*b*)	0	2·72 }		
Control incubated (*a*) ..	8	2·13	—	—
(*b*) ..	8	2·48	—	—
Az. vinelandii (*a*)	7	6·22	3·56	6·2
(*b*)	7	6·20	3·54	6·2
Az. chroococcum (*a*)	8	4·48	1·82	3·2
(*b*)	8	4·74	2·08	3·6
(*c*)	14	7·88	5·22	9·2

The sterile control medium appeared to lose a small quantity of nitrogen during incubation (cf. M. Löhnis, 1930); the initial nitrogen content has therefore been subtracted from that of the cultures. Both strains of *Azotobacter* made a good and rapid growth; *Az. vinelandii* fixed about 3·5 mgm. N after 7 days, and *Az. chroococcum* even more than 5 mgm. after 14 days. These gains corresponded to about 6 to 9 mgm. N per gm. of total organic matter present, but this was probably not all used up, and the utilization must be regarded as quite economical,

since it compares well with the utilization of glucose (Table 4).[31] This shows plainly that some of the water-soluble constituents of the straw are directly available to *Azotobacter* and may serve for the fixation of a certain amount of nitrogen (unlike the result obtained by Waksman and Hutchings, 1937). But since 50 c.c. of medium represent the soluble constituents of 5 gm. straw, even the fixation of 5·22 mgm. N corresponds to little more than 1 mgm. N per gm. of straw (incidentally, this is very similar to the gain in Exp. 2*a* with oats-straw), and under soil conditions this may easily become nullified if only small quantities of nitrate or ammonia are present and become utilized by *Azotobacter* in preference to atmospheric nitrogen; it must also be remembered that the presence of ammonia and nitrate will enable non-nitrogen-fixing organisms to compete with *Azotobacter* for the available energy material. The soil in Experiment 4 contained initially 6·2 p.p.m. NH_4– + NO_3–N, and the soils in Experiment 1 even more (see Table 28). In addition to this, some more mineral nitrogen is undoubtedly produced and re-assimilated during incubation. This makes it quite understandable that, if only the water-soluble constituents of the straw are available, *Azotobacter* may flourish abundantly in the soil without fixing nitrogen. In the artificial soil in

TABLE 22.

Multiplication of Azotobacter *and Fixation of Nitrogen in Synthetic Soil with Addition of Untreated and Water-extracted Wheat Straw.*

Treatment.	Time of Incubation.	*Azotobacter*, Thousands per gram.	
		Low Moisture.	High Moisture.
Untreated straw.	Initial	0·019	0·019
	8 days	13430·0	25740·0
	15	20088·0	57090·0
	21	23650·0	86150·0
Water-extracted straw.	Initial	0·019	0·019
	7 days	14·6	61·7
	14	24·0	36·6
	21	7·5	524·0
	28	4·8	140·0

Nitrogen-fixation (Catalyst: Se).

Treatment.	Total N., p.p.m., Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain of N., p.p.m. ($\bar{x}_2-\bar{x}_1$).	, t.	P.
Untreated, initial ..	55·9	4	13·74	—	—	—
Inc. 21 d., low moisture	66·9	3	14·25	*+11·0*	6·087	*<0·01*
Inc. 21 d., high moisture	98·0	2	8·82	*+42·1*	20·47	*<0·01*
H_2O-extracted, initial ..	42·9	4	1·38	—	—	—
Inc. 28 d., low moisture	49·0	3	2·99	*+6·1*	8·553	*<0·01*
Inc. 28 d., high moisture	51·4	3	3·98	*+8·5*	10·75	*<0·01*

[31] Some of the organic matter in the straw extract consisted of reducing sugars; another part is probably represented by gums, which are also directly available to *Azotobacter*, as shown by Mockeridge (1915).

Experiment 2*a*, on the other hand, no mineral nitrogen was present, and *Azotobacter* only had recourse to the atmospheric nitrogen, thereby causing the small gain observed.

Experiment No. 7: *Untreated and water-extracted wheat straw in "synthetic" soil.*—An artificial soil similar to that in Experiment 2*a* was made up from 85% pure sand, 14% kaolin, and 1% $CaCO_3$; to this were added 2% untreated or water-extracted straw, and 12·5% of a nutrient solution containing 0·1% K_2HPO_4, 0·05% $MgSO_4$, 0·02% $FeCl_3$, 0·01% Na_2MoO_4; the solution also included a suspension of soil from Experiment 4 (low moisture, + $CaCO_3$). Portions of 90 gm. were placed in Petri dishes, two of which were given an extra addition of 7·5% H_2O; this saturated the medium completely. Incubation at 28–30°C. with periodical plate counts of *Azotobacter* and nitrogen determination after 3 and 4 weeks gave the results shown in Table 22.

The dishes with untreated straw show an abundant development of *Azotobacter*, especially at high moisture, where the colonies became macroscopically visible on the surface. Small quantities of nitrogen are fixed; the amounts correspond to approximately 0·6 mgm. N per gm. of straw at low and 2·1 mgm. at high moisture, and are roughly proportional to the final numbers of *Azotobacter*. The theoretical numbers of *Azotobacter*-cells of normal size required to bring about this amount of fixation would be 110 mill. per gm. at low and 420 mill. per gm. at high moisture, of which thus the final plate counts account for 20–25%.

The removal of the water-soluble constituents from the straw has reduced the development of *Azotobacter* enormously, especially at low moisture, where their numbers are not much higher than may be found in natural soil. In both cases there is an apparently significant but very small gain of nitrogen (corresponding to 0·3–0·4 mgm. per gm. of straw added) which, if real, could hardly be explained as simple synthesis of *Azotobacter*-cells, especially at low moisture. The plates showed an abundant growth of excessively polysaccharide-forming bacteria similar to the "bacille gommeux" of Winogradsky (1926), which might conceivably have fixed some nitrogen here; but since the experiment was not carried out in duplicate and on rather small quantities of material, no great significance can be attached to it. Another experiment was therefore made with water-extracted straw under aerobic conditions, with larger quantities of material and a longer period of incubation. The possible influence of soil organic matter was also tested by addition of 10% of a wheat soil rich in humus (No. 81, Table 2).

Experiment No. 8: *Water-extracted wheat straw in "synthetic" ± natural soil.*—The basal synthetic soil was the same as in the previous experiment; portions of 600 gm. were given the following additions:

(*a*) 1·5% extracted straw
(*b*) Do. + 10% soil No. 81
(*c*) 10% soil alone
} + 12·5% nutrient solution and inoculum as in Exp. 7.

Incubation took place in large crystallizing dishes for 8 weeks at 28–30°C. The results are given in Table 23.

In the first series (straw alone) there is a moderate development of *Azotobacter*, as in the previous experiment, but absolutely no gain of nitrogen, which renders the significance of the previous experiment doubtful. The extra addition of humus-rich soil (ser. *b*) has reduced the development of *Azotobacter*, which hardly shows a significant multiplication, and no significant gain of

TABLE 23.

Multiplication of Azotobacter *and Fixation of Nitrogen in Synthetic Soil ± Natural Soil, with Addition of Water-extracted Wheat Straw.*

I. Multiplication of *Azotobacter*.

Time of Incubation.	Plate Counts of *Azotobacter*, 1000 per gm. of Soil.		
	Series (*a*). (Straw Alone.)	Series (*b*). (Straw + Soil.)	Series (*c*). (Soil Alone.)
Initial	0·028	0·194	0·127
8 days	39·7	(<0·7)*	0·15
28 days	18·0	0·28	0·13
42 days	14·2	0·33	0·13
56 days	12·1	0·32	0·19

II. Nitrogen content (Catalyst: Se).

Treatment and Time.	Total N, Mean p.p.m. ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.
(*a*) (straw):						
Initial	36·8	3	7·61	—	—	—
28 days..	37·5	3	2·69	+0·7	0·517	0·7−0·6
56 days..	36·0	2	0·13	−0·8	0·544	0·7−0·6
(*b*) (straw + soil):						
Initial	175·9	3	3·44	—	—	—
28 days..	178·6	3	18·17	+2·7	1·423	0·3−0·2
56 days..	177·7	3	36·35	+1·8	0·683	0·6−0·5
(*c*) (soil):						
Initial	157·6	4	85·62	—	—	—
28 days..	158·7	3	25·85	+1·1	0·305	0·8−0·7
56 days..	153·8	4	1·10	−3·8	1·414	0·3−0·2

* Too high dilution.

nitrogen has taken place. This effect can hardly be ascribed to any other cause than the provision of available nitrogen by the soil, which has enabled other organisms to suppress *Azotobacter*. The medium contained initially a mere trace of nitrate and ammonia, but in the third series (addition of soil alone) there was, after 28 days, a content of 11·9 p.p.m. NO_3–N, and after 56 days of 10·9 p.p.m. In this series the numbers of *Azotobacter* have remained practically stationary, and the nitrogen content has not changed significantly (cf. Table 7). It has been claimed by Bortels (1936) that sodium molybdate in a concentration of 0·001% will enable *Azotobacter* to assimilate free nitrogen in the presence of nitrate, although this is also largely utilized. The present findings are of some interest in showing that even a higher concentration of Na_2MoO_4 (0·01%) does not necessarily help *Azotobacter* from being suppressed by other organisms in the presence of available nitrogen and shortage of available organic food material, such as in ser. *b*.

The series of experiments, Nos. 1–8, now justifies the following conclusions:

Under aerobic soil conditions only the water-soluble constituents of oats- and wheat-straw become available to *Azotobacter*, and only in artificial soil free from mineral nitrogen do we observe a moderate fixation of nitrogen, which does not materially exceed 1 mgm. N per gm. of straw present. No fixation has ever been found to take place in the absence of *Azotobacter*, and has been found with certainty only in cases where *Azotobacter* has reached numbers incomparably higher (millions per gm.) than under natural soil conditions; thus there is nothing to suggest that organisms of other groups will utilize the organic matter of the straw for nitrogen fixation. The fact that vigorous nitrogen fixation and strong development of *Azotobacter* may be induced by extra addition of small quantities of sugar or salts of organic acids indicates that organisms capable of producing such compounds from the insoluble constituents of the straw do not develop under fully aerobic soil conditions.

When semi-anaerobic conditions are created by saturation of the soil with water, a stronger fixation of nitrogen may be induced, but this is a slow process, since 8 months at 28–30°C. were required for fixation of 6 mgm. N per gm. of oats straw in sand, and 3 months for fixation of 3 mgm. N per gm. of wheat straw in soil.

From these results it is obvious that the straw residues of wheat and oats crops do not represent a very valuable form of energy material for nitrogen fixation under the conditions normally existing in Australian wheat soils.

Besides the residues of straw and stubble, we must reckon with the organic matter of the plant roots as a potential energy material, which will always be left behind by the crops, while the greater part of the straw will usually be destroyed by stubble-burning or carried away as hay.

The value of root material of cereals for nitrogen fixation does not seem yet to have been investigated. An experiment in this direction was therefore carried out. Roots of wheat plants (from flowering to ripening stage) that had served for *Azotobacter*-counts in the rhizosphere (Table 3) were collected, dried at 98°C., and ground finely. A synthetic soil was made up from 90% pure sand, 9% kaolin, and 1% $CaCO_3$; to this were added 2·5% root material (containing 3·51% H_2O and 36·8% organic matter as loss on ignition, thus introducing 0·92% organic matter into the medium), 10% of a nutrient solution containing 0·25% K_2HPO_4, 0·1% $MgSO_4$, 0·1% $FeCl_3$, and 0·005% Na_2MoO_4, besides 1% suspension 1:5 of soil No. 44 as inoculum. Portions of 250 gm. of medium were placed in 4 glass jars similar to those used in Experiment 4, and two of the jars were given an extra addition of 8% H_2O to give complete water-saturation. They were then incubated at 28–30°C., and periodical nitrogen determinations and *Azotobacter*-counts carried out. The results are shown in Table 24.

At low moisture content there is only a moderately strong development of *Azotobacter*, but after 60 days there is quite a significant gain of nitrogen, corresponding to approximately 1·5 mgm. N per gm. of organic matter introduced with the root material. It might seem that in this case some nitrogen may have been fixed by organisms other than *Azotobacter*: the numbers of this organism seem rather too low to account for the fixation of 13·7 p.p.m. nitrogen; theoretically some 140 mill. cells of normal size would have to be produced, i.e., there should have been an average daily production of 2 mill. new cells per gm. of medium, which is about 30 to 80 times as high as the numbers observed by plate counting; but since no direct counts were carried out in this series, the question

TABLE 24.

Nitrogen-fixation in Sand-kaolin Mixture with Wheat Root Material.

Time of Incubation.	Total N, p.p.m., Mean ($\bar{x}$). Catalyst : Se.	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	*Azotobacter*, Plate Count. 1,000 per gm.
I. Aerobic conditions (10·6% H_2O).							
Initial ..	91·1	4	20·01				0·024
14 d. (*a*) ..							24·3
30 d. (*a*) ..	94·7	3	3·98	+3·6	2·152	0·1—0·05	65·2
(*b*) ..	96·3	3	57·68	+5·2	1·731	0·2—0·1	32·0
60 d. (*a*+*b*)	104·8	4	8·08	*+13·7*	8·954	*<0·01*	24·2
II. Semi-anaerobic conditions (17·1% H_2O).							
Initial ..	91·1	4	20·01				0·024
14 d. (*a*) ..							6050·0
30 d. (*a*) ..	103·2	3	5·53	*+12·1*	6·978	*<0·01*	3340·0
(*b*) ..	105·2	3	5·89	*+14·1*	8·111	*<0·01*	6660·0
60 d. (*a*+*b*)	110·6	4	5·06	*+19·5*	13·49	*<0·01*	2220·0
120 d. (*a*+*b*)	115·6	3	23·15	*+24·5*	10·92	*<0·01*	319·0

Direct counts in material under semi-anaerobic conditions :

	Total Bacteria, Mill. per gm.	*Azotobacter*-like Org., % of Total.	
30 d. (*a*)	555±42·7	5·0	Vegetative clostridia were observed only sporadically, about 0·5–1·5% of total.
(*b*)	497±38·3	6·0	
60 d.	394±29·9	5·5	

cannot be answered with certainty. A small quantity of nitrate (0·4 p.p.m. NO_3–N) was present after 60 days; it is therefore unlikely that the fixation would have proceeded beyond this stage.

Where semi-anaerobic conditions have been created by full water-saturation of the medium, we find the same effect as in the experiments with straw: *Azotobacter* develops abundantly during the first 30 days and then declines, especially in the second half of the experimental period. Nitrogen fixation is comparatively vigorous during the first 30 days, where the numbers of *Azotobacter* are highest, and then becomes slower; during the last 60 days, when the numbers of *Azotobacter* show a marked drop, the fixation amounts to only 5 p.p.m. or 20% of the total fixation. The total yield of fixed nitrogen, 24·5 p.p.m. (which corresponds to approximately 2·7 mgm. per gm. of organic matter), would theoretically require a total production of 245 mill. normal *Azotobacter*-cells per gm., or an average of

about 2 mill. new cells daily, which might well be expected in comparison with the figures shown by plate counting. The direct counts of total bacteria are comparatively low, and clostridia form only a very insignificant proportion hereof. Everything thus suggests that the fixation is entirely due to *Azotobacter*.

The general result of this experiment thus leads to the conclusion that the organic root material is not much different from the straw as a source of energy for nitrogen fixation; if only a moderate degree of fixation shall be obtained (2·5–3 mgm. N per gm. of organic matter supplied), a high degree of moisture must be maintained for a period of several months.

If we now would try to form an estimate of the quantities of nitrogen that could be fixed on the basis of the residues of straw, stubble and roots of the cereal crops (mainly wheat), we must consider (1) the amounts of organic matter represented by these residues, and (2) the soil conditions under which the decomposition of this organic matter takes place.

The amount of wheat straw may roughly be estimated at 1½ times the weight of the grain, or approximately 100 lb. straw per bushel of wheat. The weight of the roots is less easy to assess; according to Harris (1914) and numerous earlier data collected by Miller (1916), it may rise to 25% of the weight of the top portions of the plants at low yield and low soil moisture. Richardson (1923), on the other hand, found the weight of the wheat roots amounting to only 3 to 11% of the total plant. We can therefore not reckon with more than, at the most, 20% of the weight of the tops, or about 30 lb. (= 20% of 60 lb. grain plus 100 lb. straw) root material per bushel. The total 130 lb. of straw and root material will not all be returned to the soil, since in ordinary farming practice most of the straw is either burned or eaten by sheep if the stubble fields are grazed before fallowing; it is unlikely that more than one-third of the straw will be left as stubble. Generally speaking, we may say that there will be at the most some 60 to 80 lb. of root and stubble residue per bushel of wheat grain available as a potential energy material for nitrogen fixation. (This corresponds to some 700 to 1000 lb. residue per acre from an average 12-bushel wheat crop; oaten or wheaten hay crops may similarly be expected to leave some 400–500 lb. of residue per ton of hay produced).

To these amounts of residue we should correctly add the organic matter which the soil receives during the growth of the crops in the form of organic root secretions and decayed root particles. The quantity of these can only be guessed, but is hardly considerable. Lyon and Wilson (1924) found that maize plants in aseptic water culture liberated organic compounds in quantities equal to 1–3% of the dry weight of the plants; they considered it probable (although this does not seem obvious) that the yield would be higher under natural conditions. It will probably be a liberal estimate to assume that the wheat plants may give off altogether 5% of their total dry weight as root secretions plus root tissue during the growth period. This would correspond to somewhat less than 10 lb. per bushel of grain produced (= 5% of 60 lb. grain plus 100 lb. straw plus 30 lb. roots). We may safely disregard the importance of these small quantities of organic matter as energy material for nitrogen fixation, in view of the apparent unsuitability of the actual root secretions as food material for *Azotobacter*, as shown by Krasilnikov (1934), and the present observations (Table 3) which show that even under favourable soil conditions *Azotobacter* is less stimulated in the neighbourhood of the roots than is the general soil microflora.

As to the soil conditions, we may first of all safely conclude that no nitrogen will be fixed during the decomposition of the residues in the very numerous soils where acid reaction or phosphate deficiency prevents *Azotobacter* from multiplying when organic matter is made available. But even where reaction and phosphate supply are optimal, it may be difficult to have all other conditions fulfilled, especially moisture and temperature; besides, there is the disturbing influence of nitrate and ammonia in the soil,[32] which must always be expected to counteract the nitrogen fixation, if not to suppress it altogether. A degree of moisture in the surface soil, approaching saturation and persisting for longer periods (which we must consider necessary for an effective utilization of the residues), can only be expected in periods of high rainfall and low rate of evaporation, i.e. the months of June–August in districts with winter maximum of rainfall; but this is associated with a low soil temperature. Systematic observations on soil temperatures in the wheat districts of New South Wales have not yet been made. Observations in South Australia by Prescott and Piper (1930) and in Victoria by Richardson (1923) and Penman and Rountree (1932) have shown mean soil temperatures of 6·5 to 10·5°C. at a depth of 6 inches during these months, when the moisture content of the surface soil is highest. Such temperatures are definitely unfavourable for nitrogen fixation, both in pure cultures of *Azotobacter* (Burk, 1934)[33] and in the soil itself (Koch et al., 1907; Hutchinson, 1918). Higher moisture content in the subsoil may indeed exist under more favourable temperature conditions, but here there is no significant supply of organic matter from the plant residues. The nitrate concentration is lowest in soil under crops in their later stages of growth and for some time after harvesting (Prescott and Piper, 1930; Penman and Rountree, 1932), but during the growth of the crop there are only the small quantities of root material to act as energy material for nitrogen fixation, and during the later stages of growth (September–November) no high degree of soil moisture can be expected. This is even more true of the period after harvesting, when the soil is either left as stubble land or subjected to short fallowing—also of the northern parts of the wheat belt in New South Wales, where short fallowing is most common and most of the rain falls in the summer months, but the rate of evaporation is high owing to the summer temperature.

Thus we can neither in summer time (when crop residues are ploughed into the soil immediately after harvest and before short fallowing) nor in winter time (when the residues are ploughed under in the autumn before long fallowing) expect really optimal conditions for nitrogen fixation on the basis of these residues. The same applies to the stubble fields, where only the roots are actually incorporated into the soil, and where the degree of moisture is usually not high except in wet autumns. On stubble fields there is often a considerable growth of weeds, self-sown wheat, etc., parts of which will serve to augment the amount of actual crop residues when the stubble field is ploughed in the autumn; the

[32] The moisture and temperature conditions in wheat soils have been discussed by Richardson (1923), Richardson and Fricke (1931), Prescott and Piper (1930), and Penman and Rountree (1932). Data on nitrate content at different seasons have been given by Taylor (1922), Prescott and Piper (1930), and Penman and Rountree (1932). Cf. also Prescott (1934).

[33] A number of strains of *Azotobacter* from the present experiments were tested for growth at 9-11°C. Only one strain (No. 79) produced a fair but very slow growth at this temperature, and another (No. 44) a mere trace of growth. No significant activity of *Azotobacter* can therefore be expected in seasons where such soil temperatures prevail.

quantity of this material is very variable and difficult to estimate, especially as much of it is usually eaten off by sheep. Since at least some of it represents a younger type of plant material than the cereal straw and roots, it might be expected to be more easily decomposible and therefore more readily available for nitrogen fixation, but against this we must set the higher nitrogen content of young plant material (Waksman, 1932) with consequent tendency to ammonia and nitrate production; under ordinary circumstances this material can hardly be considered of much significance, especially since its decomposition will take place first during the winter months, where the moisture conditions may indeed be favourable for nitrogen fixation but under unfavourable temperature conditions, and afterwards in spring time with lower moisture and increasing nitrate production.

Even under exceptionally favourable combinations of moisture, temperature, soil reaction, supply of mineral nutrients, absence of ammonia and nitrate, etc., the total amount of crop residues would be insufficient for a nitrogen fixation equal to the nitrogen demands of the wheat crop. As mentioned above, we may reckon with a total production of some 130 lb. straw and root residue per bushel of grain; if the stubble were not burned and the residues utilized with an efficiency as high as in Experiment 4 under high moisture, i.e. 3 parts of nitrogen per 1000 parts of residue, the resulting gain would only be about 0·4 lb. nitrogen compared with the consumption of 1·2 lb. nitrogen per bushel of grain. If the stubble were burned (which is the usual practice, and necessary before short fallowing or sowing on stubble-land) there would only be 60–80 lb. residue left to give a fixation of some 0·2–0·25 lb. N compared with a consumption of about 1·5 lb. N per bushel of grain plus burned straw.

About one-third of the nitrogen content of the grain must therefore be considered the highest yield that could be expected from nonsymbiotic nitrogen fixation on the basis of the crop residues, and this only under conditions that are not commonly fulfilled in Australian wheat soils.

There is no reason to think that the residues of roots and stubble left by oats crops for hay or grazing will be qualitatively or quantitatively much different from the residues of wheat.

Generally speaking, it becomes difficult to uphold the belief in the high importance of non-symbiotic nitrogen fixation in arid soils under permanent cereal cultivation, as maintained by several American and Indian investigators (see introduction). To give a complete compensation for the nitrogen consumption represented by the grain alone (1·2 lb. per bushel) the nitrogen-fixing bacteria would have to fix approximately 10 parts of nitrogen per 1000 parts of total residue (130 lb. straw and roots per bushel of grain). This is very close to the yield in vigorous mixed cultures of nitrogen-fixing and cellulose-decomposing bacteria under laboratory conditions, and is difficult to reconcile with the results of the present experiments, which have shown so consistently that cellulosic materials serve far better as food material for nitrogen fixation under high than under low degrees of moisture.

As previously mentioned, there is no real proof that other organisms than *Azotobacter* will fix significant quantities of nitrogen under arid soil conditions. Neither is there any actual foundation for the belief that *Azotobacter* will utilize its energy material far more economically in the soil (and in arid soils especially) than in pure cultures. This appears from those experiments in the present series where nitrogen fixation was most intensive, viz. Experiments 2*a*, 4 and 5 with extra additions of small amounts of glucose or salts of organic acids.

Experiment No.	Gain of Nitrogen, mgm.	
	Per gm. of Substance.	Per gm. of Org. Carbon.
2 *a*, Glucose (av. *a* and *b*)	15·4	38·5
5, Glucose (av. *a* and *b*)	14·1	35·3
5, Ca-lactate (av. *a* and *b*)	5·96	18·6
5, Ca-acetate (av. *a* and *b*)	5·3	17·8
4, Ca-acetate (av. *a* and *b*)	3·8	12·8

The conditions for the activity of *Azotobacter* were here in every respect optimal: moderate moisture content, free access of oxygen, optimal temperature, low concentration of organic nutrients, adequate supply of calcium carbonate, phosphate and molybdenum, absence of nitrate. If the fixation takes place in field soils with the same economy as in these experiments, the annual gain of 20–40 lb. N per acre, so frequently referred to, will require the consumption by *Azotobacter* of at least 550–1100 lb. carbon in compounds equal to glucose in nutritive value, or twice this amount in compounds like lactic or acetic acid. Rather than in cultivated soils from which crops are continually carried away, such supplies of organic nutrients could be expected under prairie conditions (cf. Hall, 1905*a*) or in the leaf beds of forests (Olsen, 1932), where large quantities of plant material of a wide C/N ratio are allowed to decompose *in situ*. And also in these cases a high degree of moisture must be considered essential for an effective utilization of the cellulosic materials for nitrogen fixation, whether by *Azotobacter* or by butyric acid bacilli. Investigations on the numbers of nitrogen-fixing bacteria arising under such conditions would be a matter of great interest.

4. *Soils Exposed to Daylight.*

Now that we have seen that neither the native soil "humus" nor the crop residues provide sufficient energy material for a nitrogen fixation of any significance in comparison with the nitrogen demands of the crops, we are left with the algae as a last possible factor in non-symbiotic nitrogen fixation.

That the growth of algae may result in the addition of considerable quantities of nitrogen to soil or sand media has been shown by several investigators, of whom we need mention only Schloesing and Laurent (1892), Richter (1899), Bouilhac and Giustiniani (1901), and Wilfarth and Wimmer (1907). It has also been shown repeatedly (for references, see Waksman, 1932, and Bristol and Page, 1923) that *Azotobacter* can live in symbiosis with green algae and fix nitrogen at the expense of organic compounds elaborated by these. Some authors (e.g. Koch, cit. after Pfeiffer et al. (1910), Wilsdon and Ali (1922) and Gainey (1930) with special reference to semi-arid cultivated soils) regard this function of the algae as an important link in the nitrogen metabolism of the soil, but these statements are based more on conjecture than on quantitative experimental data. Others, e.g. Pfeiffer et al. (1910), have expressed grave doubts as to whether the, at the best, very scanty algal growth observed on cultivated soils could ever be of any importance in comparison with the luxuriant growth that is produced where even a moderate quantity of nitrogen is fixed.

No investigations have yet been carried out on the occurrence of algae in Australian wheat soils, but theoretically the prospects of a significant gain of nitrogen through the combined action of algae and nitrogen-fixing bacteria do not

seem favourable. The quantity of algal substance in the soil can only be very roughly guessed (Russell, 1937), and since the rates of death and reproduction of algal cells in the soil are unknown, we cannot, even if improved methods of counting gave us a reliable estimate of the quantity of algal matter at a given moment, calculate the amount of substance produced and again transformed in a given interval of time. But if we assume that 50% of the dry matter of the algal substance becomes available to *Azotobacter* and is used for the fixation of 20 mgm. nitrogen per gm. of organic matter, a simple calculation shows that even the moderate fixation of 10 lb. nitrogen per acre per annum will require the production of 1000 lb. dry algal matter per acre annually—a figure equal to the weight of the straw of a 10-bushel wheat crop. Such a production appears unlikely on the wheat soils, where the growth of algae is never conspicuous. To the weight of the actual cell material we should indeed add the amount of organic matter secreted by the cells during growth, but this amounts to, at the most, 30% of the cell material, and may be much less (Roberg, 1930). Our assumption of a fixation of 20 mgm. N per gm. of organic matter implies that it is all utilized by *Azotobacter* working at almost maximal efficiency; this condition can more easily be fulfilled in pure cultures than in the soil, where other organisms will compete with *Azotobacter* for the food material, particularly in the presence of ammonia or nitrate. Finally, not all the soluble compounds derived from the algae may be favourable nutrients for nitrogen fixation by *Azotobacter*; as shown by Aleyev (1934), autolysis products of algae contain certain quantities of amino-nitrogen which might interfere with the nitrogen fixation, either directly or after being broken down to ammonia or nitrate (cf. also De, 1939). Whether other organisms can assimilate nitrogen in association with algae is not known, but it seems unlikely that highly efficient organisms of this kind, if existing, should still have escaped detection. Gains of nitrogen in this way can thus only be expected in soils favourable for *Azotobacter*.

Besides through the association of algae and *Azotobacter*, nitrogen may be fixed directly by certain blue-green algae. Very little is yet known about the distribution and ecology of these organisms. If they are of common occurrence in the wheat soils, their function might possibly be of some importance. Provided the dry cell substance has a nitrogen content of 5% (which is probably rather high), a fixation of 10 lb. nitrogen per acre would involve the production of 200 lb. dry algal matter, which is not in itself an unreasonable figure, and which might not be conspicuous to the naked eye, especially if photosynthesis could take place not only on the surface, but also in the depth of the soil. It has recently been claimed by Fehér and Frank (1936*a*) that blue-green algae are capable of utilizing infra-red radiation penetrating into the deeper layers of the soil, so that photosynthesis may take place well below the soil surface. If this is the case, nitrogen fixation might conceivably also occur. This theory, however, is not supported by the earlier experiments of Schloesing and Laurent (1892) and Wilfarth and Wimmer (1907), where practically all the fixed nitrogen was present in a thin external layer of sand. The observations of Drewes (1928) are even more decisive: cultures of nitrogen-fixing blue-green algae failed to fix nitrogen under a simple cover of black paper, while even cardboard, according to Fehér and Frank (1936*a*), lets through sufficient infra-red radiation for photosynthesis. For the present we can therefore only reckon with nitrogen fixation by algae (directly or in association with bacteria) on the actual soil surface. If such a gain is observed in a laboratory experiment and we wish to express it in

terms of pounds per acre of soil, we must convert it on the basis of area and not of weight of soil.

A number of soils from Table 2 were tested for a possible gain of nitrogen through such processes; 12 wheat soils were used, besides soil No. 8 with 0·2% $CaHPO_4$, which had been found to fix nitrogen on addition of glucose. Portions of 80 to 200 gm. of air-dry soil were moistened to approximately two-thirds of their water-holding capacity and placed for a period of 3–3½ months in an attic window facing the east. No gas was burned and no chemicals used in this room, in order to minimize the danger of absorption of nitrogen compounds from the air. Petri dishes were at first used as containers for the soil, but were later replaced by 300 to 500 c.c. conical suction flasks with the neck closed with a well-fitting rubber stopper and the side tube filled with a loose plug of cotton wool. By this arrangement the atmospheric air had free access to the soil, while the evaporation of moisture, which in sunshine was undesirably strong from the Petri dishes, was reduced to a minimum. After incubation, total nitrogen was determined in the soil, and tests for *Azotobacter* and determinations of ammonia and nitrate were made in some cases. Most experiments were carried out on the same material from which the samples for the nitrogen fixation experiments without organic matter, with glucose and with straw, had been taken. As in the glucose and straw experiments, the average of all the nitrogen determinations on soil without addition of organic matter was taken as the initial content to be compared with the nitrogen content of the sample exposed to daylight. In some cases, however (Nos. 21, 23, 29 and 30), the experiment was carried out with soil that had been washed free from nitrate after incubation for 30 days at 28–30°C. By thus starting with nitrate-free soil it was hoped to enhance the chances of nitrogen fixation. Soil No. 19 was used both untreated and after incubation and washing; in the latter case it was also given an addition of 1·0% $CaCO_3$ and an inoculum of 1·0% of soil No. 8, which by then had been found to fix nitrogen in the daylight. Supplementary experiments were carried out on 3 soils with additions of small quantities of oats-straw, and on almost pure sand inoculated with soil No. 8 after incubation.

The growth of algae during the incubation was in most cases rather scanty, consisting of a few greenish or bluish-green specks of felt-like material, which were often on microscopic examination seen to contain *Oscillatoria*-like organisms; a few moss-protonemas were also sometimes seen. In some cases (Nos. 20 and 24) algal growth was not even visible. The only exceptions from the general rule were soil No. 8 and the sand inoculated therewith. The soil had on its surface quite a heavy brownish to bluish-green algal growth (see fig. 8, Pl. i), in some places forming actual gelatinous drops, and the outer layers of the sand were covered with a similar bluish-green layer. In two soils (No. 6 and No. 19 + $CaCO_3$) a few small plants of *Poa annua* developed during incubation; at the conclusion of the experiment these were separated carefully from the soil and analysed separately for nitrogen.

The results of the nitrogen determinations are shown in Table 25. A significant gain of nitrogen has only taken place in soil No. 8, where it amounts to about 6% of the initial content, and in the sand inoculated herewith. Soil No. 12 shows a definite loss of nitrogen, and the same appears at first glance to be the case in Nos. 6 and 19 + $CaCO_3$, but when allowance was made for the nitrogen found in the grass plants that had developed here, the losses were seen to be non-significant.

Table 26 shows that in No. 8 and the sand, where nitrogen fixation had taken place, all mineral nitrogen had disappeared during the incubation. In all other soils without addition of straw, some mineral nitrogen was present after incubation; in Nos. 29 and 30 there is even a strong nitrification, corresponding to about 4·5–5·5% of the total organic nitrogen. The additional experiments with addition of straw were made in order to prevent the accumulation of nitrate from interfering with the process of fixation; in view of the experiments in the previous section we may safely assume that no nitrogen fixation would take place on the basis of the straw itself. This treatment certainly results in a permanent removal of the nitrate (although not of all the ammonia), but as seen from Table 25 there is no gain of total nitrogen; indeed, No. 10 shows a loss which is probably significant (cf. Table 14).

These experiments suggest very strongly that algae do not function as an important factor in the nitrogen economy of Australian wheat soils, since there was absolutely no indication of any gain of nitrogen in 12 typical wheat soils after incubation for 3 to 4 months under conditions that may safely be assumed to be more favourable for growth of algae than those obtaining in the fields, where the soil surface for long periods is too dry for algal growth. It is important to note that this was also the case with alkaline soils from which the originally present nitrate had been removed (Nos. 23, 29, and 30, the last two of which were of a highly fertile type), and even where nitrogen-fixing blue-green algae were present, as shown below (No. 19 + $CaCO_3$, nitrate-free and inoculated with soil No. 8), or where provision was made for permanent removal of the nitrate, as in the soils with straw. On the other hand, the results with soil No. 8 and the sand medium demonstrate that the experimental technique used here is satisfactory in so far as it does permit a fixation of nitrogen associated with the growth of algae under certain conditions, which apparently are not fulfilled in the wheat soils. It is probably the presence of large quantities of available phosphate that has stimulated the rich algal growth and nitrogen fixation (cf. Wilfarth and Wimmer, 1907).

The plate counts of *Azotobacter* after incubation are shown at the bottom of Table 25. None of the figures are high, and actually the highest number is found in No. 10 + straw, where a significant loss of nitrogen seems to have taken place. In the two cases where nitrogen fixation has taken place, *Azotobacter* are few in numbers (soil No. 8) or seem quite absent (sand). This suggests strongly that blue-green algae were the primary agents of nitrogen fixation.

A crude culture of a blue-green alga (*Anabaena* sp.) was obtained from the sand by inoculating some of the green matter into Allison and Hoover's (1935) mineral solution (K_2HPO_4 0·5 gm.; $MgSO_4$ 0·2 gm.; NaCl 0·2 gm.; $CaSO_4$ 0·1 gm.; $FeCl_3$ 0·005 gm.; H_2O 1000 c.c.) with 0·005% Na_2MoO_4. Growth could be obtained on a corresponding agar medium, but was here always accompanied by bacterial growth, especially a non-spore-forming motile rod resembling *Bact. herbicola*, the elimination of which did not succeed. After three passages in the liquid medium, however, the culture was free from *Azotobacter* and clostridia, as shown by agar and solution tests, and from aerobic heterotrophic nitrogen-fixing organisms in general (Table 4). A quantitative nitrogen fixation experiment was carried out in the following medium: K_2HPO_4 1·0 gm.; $MgSO_4$ 0·5 gm.; NaCl 0·5 gm.; $CaSO_4$ 0·2 gm.; $FeCl_3$ 0·02 gm.; Na_2MoO_4 0·01 gm.; H_2O 1000 c.c. Portions of 50 c.c. in 300 c.c. Erlenmeyer flasks were sterilized and inoculated each with one loopful of the algal pellicle from a 26-days-old solution culture tested for absence of nitrogen-fixing bacteria. Two flasks were analysed for nitrogen immediately after inocula-

TABLE 25.

Changes in Nitrogen Content of Soils Exposed to Daylight.

Soil No.*	Total N, p.p.m. Mean ($\bar{x}$).	n+1.	$S(x-\bar{x})^2$.	Gain (+) or Loss (−) of N, p.p.m. ($\bar{x}_2-\bar{x}_1$).	t.	P.	Incubation Time.
24. Initial ..	392·7	10	310·1				21/7–7/11,
Inc. 109 d.	393·3	4	242·8	+0·6	0·149	0·9–0·8	1936
8. Initial ..	446·8	11	804·0				14/5–3/9,
Inc. 114 d.	474·0	5	484·0	*+27·2*	5·257	*<0·01*	1936
19. Initial ..	455·2	9	316·2				17/6–28/9,
Inc. 103 d.	459·5	4	137·0	+4·3	1·141	0·3–0·2	1936
12. Initial ..	532·2	10	459·6				8/4–27/7,
Inc. 110 d.	507·3	3	10·7	*−24·9*	5·785	*<0·01*	1936
25. Initial ..	535·7	11	980·6				10/8–23/11,
Inc. 105 d.	527·3	3	74·7	*−8·4*	1·092	0·3–0·2	1936
21. Washed :							
Initial ..	563·3	3	50·7				16/9–21/12,
Inc. 96 d.	558·8	5	162·8	*−4·5*	1·017	0·4–0·3	1936
10. Initial ..	631·9	10	1038·1				21/3–4/7,
Inc. 105 d.	627·0	3	8·0	−4·9	0·763	0·5–0·4	1936
14. Initial ..	649·3	12	2361·5				21/4–11/8,
Inc. 112 d.	653·7	3	20·7	+4·4	0·541	0·6–0·5	1936
20. Initial ..	653·1	11	1394·4				17/7–29/10,
Inc. 104 d.	650·0	5	724·0	−3·1	0·462	0·7–0·6	1936
23. Washed :							
Initial ..	694·6	5	444·8				3/9–11/12,
Inc. 99 d.	689·0	6	716·0	−5·6	0·814	0·5–0·4	1936
6. Initial ..	827·1	11	2528·8				6/2–6/5,
Inc. 90 d.	798·3	3	152·7	*−28·8*†	2·958	*0·02–0·01*	1936
29. Washed :							
Initial ..	948·2	5	544·8				13/10/36–
Inc. 98 d.	953·3	3	20·7	+5·1	0·719	0·5–0·4	19/1/37
30. Washed :							
Initial ..	1050·3	3	2·7				12/10/36
Inc. 95 d.	1044·3	3	60·7	−6·0	1·846	0·2–0·1	15/1/37
19. Washed +$CaCO_3$:							
Initial ..	454·8	4	120·8				26/9–23/12,
Inc. 88 d.	437·3	4	202·8	*−17·5*†	3·370	*0·02–0·01*	1936
Sand :							
Initial ..	36·3	2	3·7				7/12/36–
Inc. 124 d.	55·3	4	25·2	*+19·0*	8·162	*<0·01*	1/4/37
25. +0·6% straw :							
Initial ..	544·5	11	980·6				16/12/36–
Inc. 96 d.	550·3	4	212·8	+5·8	1·037	0·4–0·3	22/3/37

TABLE 25.—*Continued.*

Changes in Nitrogen Content of Soils Exposed to Daylight.—Continued.

10. +0·75% straw :							
Initial ..	642·1	10	1038·1				11/12/36–
Inc. 94 d.	624·7	3	9·7	*−17·4*	2·708	*0·05−0·02*	15/3/37
11. +1·5% straw‡ :							
Initial ..	655·0	5	826·0				12/3–30/6
Inc. 110 d.	645·7	4	416·8	−9·3	1·030	0·4−0·3	1937

Azotobacter in soil after incubation : (S+ or S− : presence or absence of *Az.* in mannite sol.).

Soil No.	*Azotobacter* per gram.	Soil No.	*Azotobacter* per gram.
8	55 (S+)	19+$CaCO_3$	0 (S+)
21	0	Sand	0 (S−)
23	380 (S+)	10+straw	1160 (S+)
25	0	11+straw	370 (S+)
29	270 (S+)	25+straw	0

* Soils No. 24, 8, 19, 12, 25, 10, 14 and 6 were incubated in Petri dishes, the rest in flasks.

† Small plants of *Poa annua* developed during incubation.

‡ After incubation aerobically for 120 days ; no nitrate or ammonia present.

TABLE 26.

Mineral Nitrogen in Soils Exposed to Daylight (p.p.m.).

Soil No.	NO_3–N.	NH_4–N.	Soil No.	NO_3–N.	NH_4–N.
24. Initial..	1·1	0	10. Initial..	4·0	4·9
Incubated	16·4	(+)*	Incubated	12·7	0
8. Initial..	3·7	6·8	14. Initial..	26·1	0
Incubated	0	0	Incubated	15·9	(+)
19. Initial..	6·0	4·0	20. Initial..	2·2	0
Incubated	4·5	0	Incubated	15·1	0
19. Washed :			23 Washed :		
Initial..	0	0	Initial..	0	(+)
Incubated	12·4	0	Incubated	(+)	(+)
12. Initial..	4·0	4·0	6. Initial..	11·5	0
Incubated	2·0	0	Incubated	7·7	0
			29. Washed :		
25. Initial..	1·8	4·4	Initial..	0	0
Incubated	24·1	(+)	Incubated	46·3	0
25. +Straw :			30. Washed :		
Initial..	1·8	4·4	Initial..	0	(+)
Incubated	0	6·7	Incubated	56·5	0
21. Washed :			Sand :		
Initial..	0	0	Initial..	0	(+)
Incubated	10·6	0	Incubated	0	0
			10. +Straw :		
			Initial..	4·0	4·9
			Incubated	0	6·2

* (+)=Qualitative test positive.

tion, four were incubated as cultures, and four as controls; two of these were given an addition of 5 c.c. conc. H_2SO_4, and two of 5 c.c. 20% NaOH, in order to serve as controls upon the quantities of ammonia and nitrous oxides, respectively, that might be absorbed from the atmosphere. The cultures were started on 8th April, 1937, and were placed in the same window where the flasks with soil had previously been kept. After 3 to 4 weeks a coherent, slimy, bluish-green pellicle developed; after 6 weeks it did not grow further, and after 8 weeks it had become brownish and rather unhealthy-looking (cf. Winter, 1935). The experiment was therefore discontinued, all cultures tested with a negative result for *Azotobacter* on dextrine agar, and total nitrogen was determined. The results are found in Table 27, first section. The gain of nitrogen in the cultures is quite striking, but neither the acid nor the alkaline control solutions have absorbed the slightest trace of combined nitrogen from the atmosphere. These facts in connection with the absence of nitrogen-fixing bacteria justify the conclusion that the alga itself is capable of nitrogen fixation.

Another crude culture of an alga of similar appearance was later obtained from soil No. 19 + $CaCO_3$. This strain was also found free from *Azotobacter* and clostridia, and was tested for nitrogen fixation in the same way, but the medium was made up with tap water, which had been observed to give a more healthy-looking growth than the distilled water. The results are given in the second section of Table 27. Practically no growth took place during the first 6 weeks of incubation (July-August) when a low temperature prevailed; the rise in temperature in September was accompanied by development of dense bluish-green pellicles in all culture flasks. The control flasks, one of which had been boiled for a few seconds after inoculation instead of receiving an addition of sulphuric acid, give some indication of a slight, perhaps not significant, absorption of nitrogen from the atmosphere. The cultures in this series were also free from *Azotobacter* at the end of the experiment; they all show gains of nitrogen, which upon the whole are higher but less consistent than in the first series. Culture *a*, which had fixed least nitrogen, also showed the smallest amount of growth. (Fig. 9, Pl. i, shows the appearance of the organism).

There is thus no doubt that organisms of this group under certain circumstances can assimilate elementary nitrogen in such quantities as to give a measurable increase in the nitrogen content of the soil, such as in soil No. 8 and the sand culture in Table 24. But it is not permissible to apply the results obtained from these media of alkaline reaction,[34] plentiful supply of available phosphate, and a surface which has artificially been kept moist and thus favourable for algal growth for 3–4 months, to the wheat soils which even under similar external conditions do not produce such a conspicuous growth of algae, which are very often of an acid reaction, in which the soil surface under field conditions is moist for short periods only (except perhaps in winter time when the temperature conditions are unfavourable; according to Allison and Hoover (1935), the optimal temperature for nitrogen-fixing blue-green algae is 28–30°C.), and where the almost constant presence of smaller or larger quantities of nitrate (Prescott, 1934; Penman and Rountree, 1932), could hardly fail to interfere with the process of fixation (De, 1939). But even if there were wheat soils where reaction and supply of mineral nutrients were adequate, and where once every year the concentration of assimilable mineral nitrogen (ammonia and nitrate) were sufficiently low and

[34] The algae studied by Allison and Hoover (1935) and Winter (1935) had optimum at pH 7-8; little or no N was fixed at pH 6·0-6·5.

TABLE 27.

Nitrogen Fixation in Cultures of a Blue-green Alga.

Ser. I. Incubated 8 weeks (4/5/37–19/6/37) in daylight.

Control Solutions.	Total N. Mgm. per Flask.	Cultures.	Total N. Mgm. per Flask.
Initial (*a*)	0·06	(*a*)	1·22
(*b*)	0·11		
Inc.+H_2SO_4 (*a*)	0·02	(*b*)	1·33
(*b*)	0·03		
Inc.+NaOH (*a*)	0·04	(*c*)	1·34
(*b*)	0·03	(*d*)	1·42
Average of controls	0·05	Average of cultures	1·33

Average gain of N per culture: 1·28 mgm.

Ser. II. Incubated 10 weeks (18/7/38–26/9/38).

Control Solutions.	Total N. Mgm. per Flask.	Cultures.	Total N. Mgm. per Flask.	Gain of N. Mgm. per Flask.
Initial (*a*)	0·05	(*a*)	1·25	1·15
(*b*) ..	0·05			
Incubated, boiled ..	0·06	(*b*)	1·92	1·82
Incubated+H_2SO_4	0·11	(*c*)	2·14	2·04
Incubated+NaOH (*a*)	0·19	(*d*)	1·94	1·84
(*b*)	0·12			
Average of controls..	0·10	Average gain		1·71

the moisture conditions sufficiently favourable to allow the formation over the whole field of a continuous sheet of nitrogen-fixing blue-green algae as heavy as that observed in the second experiment in Table 27, the resulting gain of nitrogen would be inconsiderable. The fixation amounted in this experiment to 1·15 to 2·04 mgm. per flask, in which the surface area of solution was approximately 50 cm^2. Computed on the basis of an acre of soil, this would correspond to 2·1 to 3·6 lb. per acre, which is only equivalent to the nitrogen content of two to three bushels of wheat grain.[35]

While we may thus agree with Pfeiffer et al. (1910) in concluding that the activity of algae cannot be credited with any importance in the wheat soils, it cannot be denied that these organisms may play a significant role under different conditions, for instance in freshwater lakes or in rice fields where a rich growth of algae is frequently produced during the period of water-logging (references by Russell, 1937). De (1936) observed a rich development of algae and vigorous fixation of nitrogen in suspensions of rice soils exposed to daylight, and later (1939) he isolated N-fixing blue-green algae therefrom. The classical example of growth of blue-green algae on bare volcanic soils, where a nitrogen reserve may slowly be built up through the activity of these organisms, is too well known to

[35] A similar calculation might be applied to soil No. 8 in Table 25. The actual gain of nitrogen was 2·0 ± 0·403 mgm. per 74·5 gm. dry soil in a Petri dish with internal diameter 9 cm., surface area of the soil consequently 64 $cm.^2$ On the basis of an acre of soil the gain would only correspond to 2·8 ± 0·56 lb. of nitrogen.

need comment; it is highly probable that primary nitrogen fixation by blue-green algae is responsible for much of this gain.

It may finally be mentioned that the results found with soils + straw exposed to daylight in Table 25 give no indication that the straw is utilized for photochemical nitrogen fixation, as suggested by Dhar (1937) on the basis of experiments with soil + cellulosic materials exposed to sunlight. It is true that ultraviolet radiation was almost completely excluded, but this seems also to have been the case in Dhar's experiments, and in any case this kind of radiation could not act upon organic matter incorporated in the soil, since it does not penetrate below the actual soil surface (Fehér and Frank, 1936*a*). Moreover, the possible effect of algae does not seem excluded in Dhar's experiments.

(e) Mineralization of Humus Nitrogen in Australian Soils.

The nitrate content of Australian wheat soils has been studied much more exhaustively than the question of the total nitrogen balance (for references, see Prescott, 1934). As mentioned in the introduction, fallowed land is regularly found richer in nitrate than corresponding cropped or stubble land, although these also usually contain certain small amounts of nitrate. Some experiments on the influence of moisture and temperature and the production of nitrate in a wheat soil under laboratory conditions have been carried out in South Australia by Prescott and Piper (1930), but comparative investigations on the ability of a larger number of typical wheat soils to produce nitrate and ammonia from their store of organic nitrogen are yet lacking. A series of experiments was carried out in order to supply this need.

These experiments were carried out in precisely the same way as the nitrogen fixation experiments without addition of organic matter reported in Table 7 (actually these data are nothing but the nitrogen balance in some of the experiments to be described here): duplicate portions (except for a few cases where only small quantities of soil were available) of 150 to 200 gm. of air-dry soil were moistened to about 60% of their water-holding capacity and incubated in large Petri dishes for 30 days at 28–30°C., with determination of nitrate and ammonia before and after incubation. Altogether 55 soils from Table 2 were tested.[30] In some cases the soil that had been extracted with water for nitrate determination was air-dried, re-moistened, and incubated for another period of 30 days. Soil No. 22 was received in a completely water-saturated condition, and was excessively rich in nitrate (54 p.p.m. NO_3–N, or more than 6% of its total nitrogen content); it was therefore air-dried and washed free from nitrate before starting the experiment. The results of this series of experiments are given in Table 28, where the soils are arranged in order of increasing nitrogen content.

All soils, with one exception, produced nitrate during incubation, and the initial content of ammonia, with very few exceptions, decreased or disappeared completely. The exception is represented by the strongly acid, uncultivated soil No. 3 in which, however, a considerable quantity of ammonia accumulated. The increases in mineral nitrogen (nitrate plus ammonia), or "metabolizable nitrogen" to use the term of Richardson (1938), show a very clear correlation with the contents of total nitrogen. A calculation of the correlation coefficient between these two factors shows for all the 106 observations on 55 soils the highly

[30] Some of these represent mixtures of equal parts of two samples from the same field (Nos. 51 + 52, 53 + 54, 55 + 56).

significant value of + 0·818.[37] If we omit the 7 soils outside the wheat belt (Nos. 3, 4, 5, 8, 9, 44, and 55 + 56) as well as the wheat soils Nos. 1 and 2, which had been air-dried for a long period prior to examination and may therefore have given abnormally high results (Waksman, 1932), we have left 90 observations on 46 samples representing normal soils of the wheat district. The correlation coefficient between total nitrogen content and production of $(NO_3 + NH_4)N$ is now reduced to + 0·625, which is still a highly significant value. The last column of the table shows the production of $(NO_3 + NH_4)N$ as percentage of initial *organic* nitrogen (Total N − $(NO_3 + NH_4)N$). This figure, which we might call the "coefficient of mineralization", is seen to vary from 0·14 to 5·18%, the maximum value being found in the long air-dried soil No. 1. In the large majority of the cases (64 out of 106) it lies between 1·5 and 3·0%, generally with good agreement between the two parallel dishes by which most soils are represented. If we take the average of the parallels, we find the following:

Range of Coefficient of Mineralization. Per cent.	Frequency.	
	All 55 Soils.	46 Fresh Wheat Soils.
0–0·5	2	2
0·51–1·0	3	3
1·01–1·5	8	7
1·51–2·0	14	12
2·01–2·5	10	9
2·51–3·0	5	4
3·01–3·5	5	5
3·51–4·0	2	0
4·01–4·5	5	4
4·51–5·0	0	0
5·01–5·5	1	0
Total	55	46

There is here no indication of any excessively rapid nitrification of the humus nitrogen, such as has occasionally been stated to take place in arid and semi-arid soils from North America. For instance, Lipman et al. (1916), in California, found in certain cases up to 50% of the total nitrogen in soil of low humus-content nitrified after 1 month, and Gainey (1936), in Kansas, found that "normal" soils (apart from "fertility spots" with excessive nitrification) could nitrify up to 20% of their nitrogen in 4–6 weeks. There is a much better agreement between the present results and those of similar nitrification experiments by Hall (1922) in South Africa: 54 soils of different character were incubated for 30 days at 28°C., or for 6 weeks at room temperature. Four soils were found incapable of producing nitrate, while in the remaining 50 soils from 0·1 to 5·1% of the total nitrogen was transformed into nitrate, with a clear correlation between the nitrogen content of the soil and the amount of nitrate produced.

There is no obvious correlation between the coefficient of mineralization and general soil type, content of total nitrogen (as also in Hall's experiments), or even hydrogen-ion concentration; indeed, such strongly acid soils as Nos. 4, 5, 7,

[37] Soil No. 35 with extra addition of calcium carbonate has not been included in this calculation.

TABLE 28.

Production of Mineral Nitrogen in Soils Incubated 30 Days at 28–30° C.

Soil No.	Total N. p.p.m.	Before Incubation.			After Incubation.			$(NO_3+NH_4)N$ produced.	
		NO_3–N p.p.m.	NH_4–N p.p.m.	NO_3–+ NH_4–N p.p.m.	NO_3–N p.p.m.	NH_4–N p.p.m.	NO_3–+ NH_4–N p.p.m.	p.p.m.	% of Initial Organic N.
31	183	1·8	3·5	5·3	11·6 11·5	2·0 1·5	13·6 13·0	8·3 7·7	4·66 4·33 } 4·5
33	228	3·8	3·4	7·2	9·0 7·5	0 0	9·0 7·5	1·8 0·3	0·81 0·14 } 0·5
32	243	1·8	5·8	7·6	9·3 7·6	3·9 2·8	13·2 10·4	5·6 2·8	2·37 1·19 } 1·8
24	393	1·1	0	1·1	8·5 8·4	0 0	8·5 8·4	7·4 7·3	1·89 1·86 } 1·9
72	428	0·5	8·4	8·9	27·1 22·0	1·8 2·1	28·9 24·1	20·0 15·2	4·76 3·62 } 4·2
*8	447	3·7	6·8	10·5	19·5 17·7	0 0	19·5 17·7	9·0 7·2	2·07 1·63 } 1·8
19	455	6·0	4·0	10·0	22·0 22·4	0 0	22·0 22·4	12·0 12·4	2·70 2·78 } 2·7
12	533	4·0	4·0	8·0	16·6 16·4	0 0	16·6 16·4	8·6 8·4	1·64 1·60 } 1·6
25	536	1·8	4·4	6·2	22·4 22·0	1·4 3·1	23·8 25·1	17·6 18·9	3·32 3·56 } 3·4
58	556	0	0	0	18·1 17·2	0 0	18·1 17·2	18·1 17·2	3·25 3·09 } 3·2
57	563	0	2·6	2·6	15·6 14·9	0 0	15·6 14·9	13·0 12·3	2·32 2·19 } 2·3
21	583	5·3	2·7	8·0	11·9 12·6	0 0	11·9 12·6	3·9 4·6	0·68 0·83 } 0·8
37	621	5·4	2·8	8·2	32·9 31·4	1·8 2·1	34·7 33·5	26·5 25·3	4·32 4·13 } 4·2
10	632	4·0	4·9	8·9	19·9 19·2	0 0	19·9 19·2	11·0 10·3	1·76 1·65 } 1·7
11	634	6·4	5·4	11·8	24·6 22·3	3·4 0	28·0 22·3	16·2 10·5	2·60 1·69 } 2·1
13	643	4·3	5·3	9·6	30·0 32·3	0 0	30·0 32·3	20·4 22·7	3·22 3·58 } 3·4
14	649	26·1	0	26·1	31·1 32·4	0 0	31·1 32·4	5·0 6·3	0·80 1·01 } 0·9

TABLE 28.—*Continued.*

Production of Mineral Nitrogen in Soils Incubated 30 Days at 23–30° C.—Continued.

53+54	650	0·7	0	0·7	13·6 13·7	0 0	13·6 13·7	12·9 13·0	1·98 2·00	2·0
20	653	2·2	0	2·2	13·7 14·5	0 0	13·7 14·5	11·5 12·3	1·77 1·89	1·8
38	664	6·5	4·2	10·7	24·5 24·8	2·2 1·6	26·7 26·4	16·0 15·7	2·45 2·40	2·4
*3	688	0	5·9	5·9	0 0	22·9 21·4	22·9 21·4	17·0 15·5	2·49 2·27	2·4
35	715	5·1	8·1	13·2	16·9 15·7	0 0	16·9 15·7	3·7 2·5	0·53 0·36	0·4
35+1% $CaCO_3$	711	5·1	8·1	13·2	36·0 37·5	2·0 0	38·0 37·5	24·8 24·3	3·55 3·48	3·5
49	721	3·5	4·0	7·5	17·6 15·9	2·0 0·9	19·6 16·8	12·1 9·3	1·70 1·30	1·5
7	732	23·0	0	23·0	45·9 51·6	10·8 0	56·7 51·6	33·7 28·6	4·75 4·03	4·4
34	745	9·4	10·9	20·3	34·9 31·7	0 0	34·9 31·7	14·6 11·4	2·01 1·57	1·8
23	749	4·3	0	4·3	26·8 25·4	0·7 1·1	27·5 26·5	23·2 22·2	3·11 2·97	3·04
15	755	25·4	5·7	31·1	39·5 36·8	0 3·0	39·5 39·8	8·4 8·7	1·16 1·20	1·2
27	790	3·2	3·7	6·9	21·7 20·5	0 0	21·7 20·5	14·8 13·6	1·89 1·74	1·8
50	795	1·7	0	1·7	16·9 17·2	0 0	16·9 17·2	15·2 15·5	1·92 1·96	1·9
1	798	9·6	0	9·6	50·4	0	50·4	40·8	5·18	5·2
39	798	9·2	3·8	13·0	32·0 32·0	1·7 0	33·7 32·0	20·7 19·0	2·64 1·74	2·2
22	813	0	13·0	13·0	28·8 34·2	3·0 2·1	31·8 36·3	18·8 23·3	2·35 2·91	2·6
51+52	816	1·1	0	1·1	20·0 16·2	0 0	20·0 16·2	18·9 15·1	2·32 1·85	2·09
6	827	11·5	0	11·5	25·9 27·5	0 4·6	25·9 32·1	14·4 20·6	1·77 2·53	2·2
73	836	0·4	6·5	6·9	23·2 23·5	1·2 0	24·4 23·5	17·5 16·6	2·11 2·00	2·1
71	933	18·4	2·9	21·3	26·6	0	26·6	5·3	0·58	0·6
70	961	2·8	2·6	5·4	18·7	0	18·7	13·3	1·39	1·4

TABLE 28.—*Continued.*

Production of Mineral Nitrogen in Soils Incubated 30 Days at 28–30° C.—Continued.

Soil No.	Total N, p.p.m.	Before Incubation.			After Incubation.			$(NO_3+NH_4)N$ produced.	
		NO_3–N p.p.m.	NH_4–N p.p.m.	NO_3–+ NH_4–N p.p.m.	NO_3–N p.p.m.	NH_4–N p.p.m.	NO_3–+ NH_4–N p.p.m.	p.p.m.	% of Initial Organic N.
29	964	9·3	1·7	11·0	26·2 26·0	0 0	26·2 26·0	15·2 15·0	1·59 1·57 } 1·6
36	985	26·2	11·9	38·1	72·3 68·0	1·8 0	74·1 68·0	36·0 29·9	3·80 3·16 } 3·5
69	986	0	6·7	6·7	24·8 22·6	0 0	24·8 22·6	18·1 15·9	1·85 1·61 } 1·7
68	1053	0	0	0	22·3 22·8	0 0	22·3 22·8	22·3 22·8	2·12 2·14 } 2·13
30	1072	8·4	1·5	9·9	27·2 25·7	1·5 1·9	28·7 27·6	18·8 17·7	1·77 1·74 } 1·8
*55+ 56	1152	7·6	5·8	13·4	33·6 33·2	0 0	33·6 33·2	20·2 19·8	1·77 1·74 } 1·8
2	1257	10·9	0	10·9	61·0	0	61·0	50·1	4·01 4·0
26	1265	6·5	0	6·5	32·9 32·9	1·5 2·7	34·4 35·6	27·9 29·1	2·24 2·30 } 2·3
66	1508	5·2	7·0	12·2	43·2 40·5	2·4 0	45·6 40·5	33·4 28·3	2·23 1·89 } 2·1
28	1573	3·9	4·4	8·3	26·8 26·3	1·7 1·5	28·5 27·8	20·2 19·5	1·29 1·24 } 1·3
16	1604	11·3	4·0	15·3	33·3 29·7	0 0	33·3 29·7	18·0 14·4	1·13 0·96 } 1·0
*44	1728	0	3·6	3·6	27·9 28·8	0 0	27·9 28·8	24·3 25·2	1·41 1·46 } 1·4
64	1822	2·5	0	2·5	23·5 20·0	0 0	23·5 20·0	21·0 17·5	1·15 0·96 } 1·1
17	1900	12·1	5·9	18·0	34·7 45·2	5·9 5·9	40·6 51·1	22·6 33·1	1·20 1·76 } 1·5
18	2060	46·1	6·7	52·8	94·4 89·9	2·7 3·0	97·1 92·9	44·3 40·1	2·21 2·00 } 2·11
*5	2710	24·4	14·7	39·1	135·4 125·3	8·4 6·7	143·8 132·0	104·7 92·9	3·92 3·48 } 3·7
*4	3280	45·9	30·8	76·7	207·3 166·6	7·6 7·7	214·9 174·3	138·2 97·6	4·32 3·05 } 3·7
*9	5860	20·7	10·2	30·9	189·2 194·0	5·8 6·0	195·0 200·0	164·1 169·1	2·82 2·91 } 2·9

TABLE 28.—*Continued.*

Production of Mineral Nitrogen in Soils Incubated 30 Days at 28–30° C.—Continued.

Second period of 30 days.

58	556	0	0	0	13·0	0	13·0	13·0	2·34
14	649	0	0	0	9·7	0	9·7	9·7	1·56
15	755	0	0	0	12·2	0	12·2	12·2	1·68
71	933	0	0	0	5·1	0	5·1	5·1	0·56
70	961	0	0	0	9·3	1·9	11·2	11·2	1·17
64	1822	0	0	0	16·9	0	16·9	16·9	0·93

Soils marked * are outside the wheat belt.

36 and 58, of pH 4·7 to 5·5, have shown a remarkably vigorous production of mineral nitrogen practically all consisting of nitrate. It is interesting to note that the three soils from Rutherglen Exp. Farm, Vic., viz., Nos. 25, 36, and 37, are among the most vigorously nitrifying soils and transform 3·2–4·3% of their organic nitrogen into nitrate in 30 days; the particular aptitude for nitrification which these soils seem to possess may be the explanation why nitrogenous fertilizers have always at this locality failed to increase the yield of wheat even when sown on stubble land. This circumstance deserves attention in future field trials with nitrogenous fertilizers.

The appendix to Table 28 shows that the nitrate produced during the first 30 days of incubation does not represent a separate, especially rapidly decomposible proportion of the humus nitrogen; when it is removed by washing and the soil is re-incubated, the mineralization goes on at about the same rate as in the first period. By prolonged incubation it is probable that the process would slow down (cf. Russell and Richards, 1920; Fraps, 1920).

The conditions under which the soil samples were kept in these experiments are comparable with those obtaining in fields under bare fallow in summer time with good conservation of the moisture. The experimental results justify the conclusion that under this treatment all normal Australian wheat soils may be expected to convert a smaller or larger percentage of their humus nitrogen into nitrate ready to be taken up by the subsequent wheat crop. The very significant correlation between production of mineral nitrogen and content of total nitrogen in the nitrification experiments suggests that in soils under equal treatment we may expect the quantity of nitrogen produced during fallow to be roughly proportional to the humus content of the soil. Richardson and Gurney's (1934) explanation for the ineffectiveness of nitrogenous fertilizers on fallowed land, viz., the higher nitrate content in this than in stubble land, would thus seem to have a general application. But higher crop yields after fallowing do not necessarily mean that any actual "recuperation" of the fertility of the soil has taken place—they may equally well indicate stronger exploitation of the nitrogen resources of the soil (cf. Pfeiffer, 1904).

PRECIPITATION AND LEGUMINOUS PLANTS AS SOURCES OF NITROGEN.

We have now seen that non-symbiotic nitrogen fixation can never be expected to cover the whole nitrogen consumption of the wheat crops, and only under exceptional circumstances a small fraction of it, while in the average wheat soils under the system of cultivation usually adopted in New South Wales it cannot even be assumed that any nitrogen will be gained through this process at all.

But before we try to form a general picture of the nitrogen economy of the wheat soils, we must consider the existence of certain other factors counterbalancing the loss of nitrogen due to cultivation.

The first of these is the rain water, which is known to contain certain amounts of combined nitrogen, chiefly as nitrous oxides produced by electric discharges in the atmosphere. Data on amounts of nitrogen annually added to the soil by rain in various parts of the world have been collected by Miller (1913), but the question has not yet been studied systematically in Australia. The only observations here are due to Brünnich (cit. after Miller, 1913), who carried out analyses of the rain water in three localities in Queensland; one of these—Roma—was within the wheat district. The amount of nitrogen annually brought down by the rain was estimated at 3·1 to 4·1 lb. per acre, a figure very similar to that which has been found in other parts of the world away from industrial centres. It may therefore be a conservative estimate to reckon with an annual gain of 3 lb. nitrogen per acre from the rain. While this is insignificant in districts where the average yield of wheat is as high as 15–20 bus., it may be relatively important where the average yield is as low as 8–10 bus., particularly if a crop is taken only every second year (an 8 bus. crop would consume little more than 12 lb. N per acre, half of which might thus be compensated by two years' rainfall). In no case, however, can we consider this more than a contributing factor in maintaining the nitrogen supply of the soil.

A far more important factor is the symbiotic nitrogen fixation by leguminous plants. On the areas devoted to wheat cultivation in New South Wales legumes are rarely sown, except where the land is laid down to pasture, usually with mixtures of grasses and clovers, or with lucerne. On the other hand, growth of self-sown clovers and trefoils is common on land under the usual wheat-fallow or wheat-oats-fallow rotation, and especially on land left as pasture after cereal crops. Howell (1911) called attention to this phenomenon in Victorian wheat soils, and mentioned the possibility that it might suffice to cover the losses of nitrogen caused by wheat cultivation. According to Breakwell (1923), the most common wild legumes in the wheat district of New South Wales are Burr trefoil (*Medicago denticulata*) and Ball clover (*Trifolium glomeratum*), which may occur both in the wheat crops and among the herbage on the stubble fields, but reach their richest development on land left undisturbed for a couple of years after fallowing for two or three wheat crops. Breakwell mentions this practice as most successful in improving the yields of wheat in the south-western and Riverina districts of New South Wales, and suggests the sowing of these species on such laid-out land. No systematic work on the distribution and density of these plants on the wheat lands of New South Wales has yet been undertaken. An inquiry among various field officers of the Field Branch of the Department of Agriculture of N.S.W. in March–April 1938[38] elicited the general answer that where moisture conditions had permitted a growth of clovers and trefoils, it was mainly confined to the better types of soil and appeared generally to be stimulated by the use of phosphatic fertilizers, but did mostly not become heavy except on undisturbed land (Riverina, cf. Breakwell, 1923), since the winter-ploughing of the fallows tends to check the growth. In the northern districts, where short fallowing is the general rule, fair growth was sometimes reported in the wheat crops, especially on black soils in the New England–Inverell districts; an abundance of *Medicago denticulata*, *lupulina* and *maculata* were said to occur among the crops here.

[38] Through the courtesy of Mr. H. C. Stening, Chief Agricultural Instructor, Department of Agriculture, N.S.W.

The importance of these plants in adding nitrogen to the soil is difficult to estimate.[39] We have no knowledge of the actual proportion of the wheat area where wild legumes occur at all, nor any quantitative data on the mass of growth that they produce where they occur. Further, their development varies greatly with the season, and fields where they grow well are usually grazed by sheep, so that not all the legume-nitrogen is returned to the soil; other complicating factors are the proportion of nitrogen taken from soil and from the atmosphere (which may vary greatly with the conditions of growth, and especially the nitrate content of the soil), as well as the problem whether the legumes may actually by root-secretion supply nitrogen directly to the wheat plants when occurring in the wheat crops.

All these problems (distribution and numerical representation of wild legumes, production of organic matter, capacity for nitrogen fixation, possible nitrogenous root secretion, etc.) need systematic and intensive study.

Until this has been undertaken, we can only say in a general way, that where spontaneous growth of legumes takes place, it is likely to add some nitrogen to the soils, but this remains an unknown quantity, and in ordinary cropping systems with alternating cereals and fallow it is more than unlikely that it would suffice to cover the nitrogen demands of the crops, especially since the legumes mainly appear on the better type of lands, where a comparatively high yield of wheat may be expected. If the land is worked on a short-fallow system, the growth of the legumes is almost confined to the crops, where their nitrogen fixation may be considerable, but of the quantitative aspect of this we can form no opinion. Under long-fallowing, which is common in the southern parts of New South Wales with summer minimum of rainfall, germination of the legumes on the stubble fields usually starts with the autumn rains, and the plants do not reach any considerable size before they are ploughed under in the early winter and thus do not reach the period where most nitrogen is fixed; in this case also grazing is common. Here, as before, it holds that we can form no idea *a priori* of the possible importance of legumes growing in the wheat crops.

Where legumes are sown or where wild legumes produce a good growth on land allowed to revert to pasture for a year or two, things may of course be entirely different; but it must be left to future investigations (which are urgently needed) to inform us on the gains of nitrogen that may be expected here.

General Conclusions.

Where soil erosion has not set in, the nitrogen consumption of the cereal crops must be regarded as the chief source of loss of nitrogen. Actual leaching of nitrate by rains appears unlikely, although the nitrate may be washed into the subsoil (whether the disappearance of nitrate, which according to Penman and Rountree (1932) may take place here, represents an actual loss or merely a transformation of nitrate, remains to be decided). On this assumption we may try to estimate the loss of soil nitrogen under wheat cultivation.

i. If wheat, or wheat followed by oats, is grown alternately with bare fallow, long or short, the resulting loss of nitrogen to the soil may, apart from exceptional cases where it is to a small extent offset by non-symbiotic fixation, be expressed simply as (N in grain + N in straw burned or harvested as hay) — (N in seed + N in rain falling during the rotation).

[39] Few attempts have been made to estimate the gains of nitrogen by wild legumes. Alway and Pinckney (1909) suggested (very approximately) an annual gain of 8 lb. N per acre under prairie conditions.

This difference, which in normally yielding fields will always be positive,[40] must be covered by nitrogen taken from the soil's store of humus. In the simplest case—wheat alternating with long fallow—an average wheat crop of 12 bus. per acre every second year might thus be estimated to cost the soil:

N in grain	14 lb.
N in burned straw	4 lb.
Sum	18 lb. N per acre

offset by:

N in seed	1 lb.
N in two seasons' rain 2 × 3 =	6 lb.
Sum	7 lb.

i.e. a net loss of 11 lb. N per crop, or 5·5 lb. per acre per annum. This is equivalent to the nitrogen content of 96 lb. soil organic matter, if we reckon with a C/N ratio of 10:1 and a factor of 1·75 for conversion of carbon into total organic matter (Waksman, 1932). With increasing yield the balance becomes increasingly unfavourable, owing to the proportionately smaller offset by nitrogen in seed and rain.

ii. Under a similar system of cultivation, but where legumes appear on fallowed land or among crops, the loss of nitrogen may be somewhat further compensated by the legumes, largely dependent on the growth that these plants make, but it is impossible to tell beforehand whether this compensation will be complete.

iii. If the cereal crops alternate with pastures where leguminous plants succeed well, it is possible, but by no means certain, that the nitrogen fixation by the legumes will be sufficient to cover the nitrogen consumption by the cereal crops (among other things, this will depend on the ratios between the quantities of organic matter produced by cereals, grasses, and legumes, as well as upon the extent to which the pastures are grazed).

Examples i and ii represent the most common state of affairs in New South Wales. We may conclude that the former case certainly, and the latter probably, represents a gradual spending of the nitrogen reserves of the soil or a "depletive cultivation",[41] which is rendered possible through the decomposition of a part of the humus resulting in nitrate production, especially under fallow, but which will ultimately lead to impoverishment of the soil through simple lack of nitrogen, if it has not before then resulted in erosion. It is a common experience that the tendency to this phenomenon arises after a shorter or longer period of cultivation and consequent alteration of the physical structure due to loss of organic matter.

The fact that the average wheat yield in New South Wales remains fairly constant and still largely depends on climatic factors and especially rainfall, must thus be ascribed to other factors than maintenance of soil fertility under the common system of cultivation. Firstly, the generally low yields of wheat make the nitrogen depletion of the soil a slow process. Let us imagine a soil that in a virgin condition contains 0·12% total N in the upper 6 inches, where the store of humus-N can then be estimated at 2400 lb. per acre; even if this soil for 40 years has produced an average wheat crop as high as 30 bus. every second year (which corresponds to an average consumption of about 45 lb. nitrogen), the resulting decrease in nitrogen content would be 900 lb. per acre, and the soil

[40] A small gain of nitrogen from the rain might result in seasons of actual crop failure caused by drought in the growing season and sufficient rainfall to bring down a normal quantity of nitrogen outside this period.

[41] This term might be suggested as an equivalent for the German "Raubbau".

would still contain 0·075% humus N, not even allowing for the nitrogen added by the rain or the possible utilization of nitrogen in the subsoil.[42] With an average yield of the normal 12 bushels the depletion would of course be very much slower, even on a poorer soil. Secondly, it is to be remembered that the wheat area in New South Wales has been extended greatly during the period from 1901 to 1926; this implies that large areas of new land have been taken under cultivation and thus have been subject to depletive cultivation for comparatively short times. And finally, improved methods of cultivation as well as improved varieties of wheat as regards both yield and resistance to drought and diseases, have undoubtedly done much to counterbalance the effects of decreasing humus and nitrogen content.

But it cannot be doubted that a smaller or larger loss of this nature is the general rule in soils under pure cereal-fallow cultivation—a loss which, if not remedied, must inevitably result in unproductiveness even of the rich soils in northern New South Wales. The remedy most immediately suggesting itself would be a scheme of rational cultivation of leguminous plants. Crops like field peas and soy beans are generally considered unsuitable, *inter alia*, because of their heavy demand on the soil moisture, and the ordinary fallowing system leaves only brief periods for growth of clovers and related plants (in the autumn on stubble fields, and in the spring and summer among the wheat crops, where a heavy growth is undesirable as competing with the wheat for the moisture). The only practicable way would therefore seem to be a periodical laying-down of the wheat lands to pastures sown with legumes. This laying is already, as mentioned above, practised to some extent in New South Wales, but might be improved greatly by sowing leguminous plants instead of letting them appear spontaneously (as suggested by Breakwell, 1923). The choice of the kind of legumes, the length of time that the land should be left as pasture, the extent to which it should be grazed, etc., must necessarily vary with the conditions, and must be decided by field experiments.

Where experience shows that leguminous plants will not succeed it will be necessary to resort to artificial nitrogenous fertilizers. But it must be kept in mind that inorganic nitrogenous fertilizers would merely compensate the soil for the nitrogen carried away by the crops, and their use alone in a pure cereal-fallow rotation could not be expected to lessen the danger of soil erosion due to the humus destruction which is especially rapid in warm and dry climates (Jenny, 1930), and which must always be expected during fallow. Some supply of organic matter to the soil must therefore be provided, perhaps in the form of legume-free pastures with nitrogenous fertilizers, unless it be found possible to return the straw to the soil instead of burning it.

As to the question of stubble-burning in general, this practice may probably, unless industrial uses can be found for the straw, under most conditions be continued with advantage. The waste of nitrogen which it involves is comparatively small and may be estimated at rather less than 0·4 lb. per bushel of grain produced; this could easily be made good by rational legume cultivation, or would represent only a small cost in nitrogenous fertilizers. The value of stubble-burning in checking fungal diseases is generally recognized; besides, it may be of advantage in other respects. The heating which the soil undergoes during the burning possibly acts as a partial sterilization stimulating nitrification during the

[42] Cf. the lysimeter experiments at Rothamsted (Russell and Richards, 1920) in which a soil with originally 0·146% N after leaching by rain for 47 years still produced sufficient nitrate for an annual wheat crop of 15 bus.

subsequent fallow (cf. Burgess, 1929, on the effect of grass fires on soil). If undertaken before laying the land down to pasture, stubble-burning might perhaps also be beneficial by encouraging the subsequent growth of legumes (Greene, 1935).

Field experiments on the value of these different measures in maintaining crop yields and soil fertility as well as in restoring impoverished soil must be considered a vital necessity, and should be undertaken on an extensive scale.

Summary.

The present work comprises two main sections: (1) the distribution and numbers of nitrogen-fixing bacteria in Australian wheat soils, and the nitrogen-fixing capacity in pure culture, and (2) nitrogen fixation experiments with soils under laboratory conditions, supplemented with experiments on nitrification in soils under laboratory conditions.

(1). *Azotobacter* was found in 27 out of 85 soil samples, 72 of which were taken from the wheat belt; 12% of the soils of pH 6·0 and less, and 50% of the soils of pH above 6·0, contained *Azotobacter*, mostly sporadically or in numbers less than 20 colonies per gm. of soil. Numbers of 600 to 2300 per gm. were only found in 4 soils of approximately neutral to alkaline reaction and high humus content; only one of these was a wheat soil.

Plate counts on dextrine agar gave statistically valid expressions for the density of *Azotobacter*-colonies, but Beijerinck's solution method seemed more adequate for detecting a sporadic occurrence of *Azotobacter*.

Az. chroococcum was by far the most common species. *Az. Beijerinckii* was found only occasionally and *Az. vinelandii* only once.

Anaerobic nitrogen-fixing bacteria of the butyric acid bacilli group seemed to be of almost constant occurrence in the soil.

Azotobacter was not found in the rhizosphere of wheat plants taken from soils otherwise free from *Azotobacter*. In the rhizosphere of wheat plants from an alkaline soil the numbers of *Azotobacter* were only slightly higher than in the adjacent soil, whereas the general soil microflora was far richer in the rhizosphere.

Twenty-four strains of *Azotobacter* showed a normal nitrogen-fixing capacity (9 to 18 mgm. N per gm. of glucose consumed) in pure culture. There was no evidence of a particularly economic utilization of the sugar in young cultures. Several other organisms were tested with a negative result.

(2). Nitrogen fixation experiments with soils under laboratory conditions gave the following results:

(*a*) No gain of nitrogen beyond the limits of the analytical error could be detected in 33 soils incubated for 30 days at 28–30°C. with a moderate degree of moisture, even if *Azotobacter* had multiplied vigorously during incubation. Attention is called to certain technical errors which may give rise to fictitious gains of nitrogen. A survey of the numerous statements in the literature concerning nitrogen fixation in soil incubated without addition of organic matter makes it appear questionable whether this has ever been proved with full certainty.

(*b*) Fifteen wheat soils incubated under similar conditions with addition of glucose showed mostly none or, at the best, a slight nitrogen-fixing capacity. Where nitrogen fixation took place there was always a strong multiplication of *Azotobacter* as shown by both cultural and microscopic tests; a considerable multiplication of *Azotobacter* could on the other hand take place without being accompanied by any nitrogen fixation. A control soil of alkaline reaction and high phosphate content fixed about 6 mgm. N per gm. of glucose and showed a stronger development of *Azotobacter* than any of the wheat soils. The failure

of neutral or alkaline soils to fix nitrogen on glucose addition must be ascribed to phosphate deficiency. Under anaerobic conditions, where up to 4 mgm. N per gm. of glucose could be fixed, the microscopic picture was entirely dominated by vegetative clostridia, which otherwise were hardly ever seen.

(*c*) Soils with addition of oats or wheat straw incubated under aerobic conditions for periods up to 4 months showed no gain (sometimes a loss) of nitrogen, even where the growth conditions were made optimal for *Azotobacter*, and where this organism existed for months in numbers of millions per gm. of soil. In corresponding experiments with artificial humus-free soil a fixation of 0·5–1·0 mgm. N per gm. of straw could take place. Larger gains of nitrogen were found in water-saturated media after prolonged incubation; these gains could reach 3 mgm. per gm. straw in soil after 3 months, and 6 mgm. per gm. straw in and after 8 months. This seems to be due to a more copious formation of organic acids, etc., as metabolic by-products in the anaerobic decomposition of the straw in the water-saturated medium, which by-products are utilized by *Azotobacter* on the surface of the medium; clostridia were little in evidence under these conditions. In fully aerated soil only the water-soluble constituents of the straw become available to *Azotobacter*.

Experiments with root-material of wheat gave results not essentially different from those found with straw. A high degree of soil moisture seems generally necessary for an effective utilization of cellulosic materials for nitrogen fixation.

Where nitrogen fixation took place it was, as in the experiments with glucose, always accompanied by a multiplication of *Azotobacter*, which reached numbers incomparably higher (ten thousands to millions per gm. of soil) than ever found under field conditions. Generally the numbers of this organism, as revealed by both microscopic and plate counts, were so high as to suggest that the process of nitrogen fixation consisted in a simple synthesis of *Azotobacter*-cells; only a few experiments with artificial soil gave some suggestion of small gains of nitrogen through other processes.

The most efficient nitrogen fixation observed in soil was 14–15 mgm. N per gm. of glucose and 5–8 mgm. per gm. of acetic or lactic acid, which is very similar to the yields in vigorously fixing pure cultures of *Azotobacter*. There is thus no evidence that *Azotobacter* will necessarily utilize its nutrients more economically in the soil than in pure cultures.

(*d*) Wheat soils exposed to daylight for periods of 3 to 4 months showed no gains due to the development of algae. In experiments with another soil and with sand medium, small quantities of nitrogen were fixed apparently by blue-green algae. Even the highest gains of nitrogen in the cultures would correspond to only small quantities in the field, where the conditions are rarely favourable for nitrogen fixation by algae; this process cannot therefore be credited with any significance in the wheat soils.—It cannot be regarded as proved that nitrogen is fixed in the soil by photochemical processes, as maintained by Indian investigators.

(*e*) Fifty-five soils of different character, including 46 wheat soils, showed after incubation for 30 days at 28–30°C. a production of nitrate and ammonia roughly proportional to the nitrogen content of the soil. In the wheat soils the correlation coefficient between produced $(NO_3 + NH_4)$—N and total soil nitrogen amounted to +0·625. From 0·1 to 5·2, in most cases 1·5 to 3·0% of the initial organic ("humus") nitrogen was converted into mineral N, chiefly nitrate; there was little or no accumulation of ammonia.

As a general conclusion there seems to be no foundation for the frequently expressed opinion that soils from arid climates have an extraordinary nitrogen-fixing power and may, through the utilization of crop residues by free-living nitrogen-fixing organisms, be permanently under cereal cultivation without depletion of nitrogen. In Australian wheat soils we can normally expect no gain at all and only under exceptionally favourable circumstances a fixation corresponding to one-third of the nitrogen requirements of the crops on wheat land worked on the usual wheat-fallow rotation. The importance of non-symbiotic nitrogen fixation in nature is probably largely confined to uncultivated soils where no crops are carried away and the vegetable debris is allowed to decompose *in situ*.

The practice of growing wheat alternating with fallow and without use of nitrogenous fertilizers must be regarded as a gradual consumption of the nitrogen reserves of the soil, from which some nitrate is produced during fallowing. This consumption is only incompletely compensated by non-symbiotic nitrogen fixation and the effect of the rain, and if continued it must in time lead to permanent loss of fertility. The natural remedy must be looked for in the introduction of leguminous crops in the rotations, or a judicious application of nitrogenous fertilizers where this is not practicable. Investigations into these problems as well as the possible importance of wild legumes on the wheat fields are urgently required.

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EXPLANATION OF PLATE I.

Figs. 1-2.—Plate counts of *Azotobacter* on dextrine agar. Inc. 6 d. 28-30°C. 1, normal soil (No. 44, Table 3, 20/10/1937), dil. 1 : 50; 2, soil with addition of wheat straw plus 0·5% Ca-acetate (Table 18), dil. 1 : 1,000,000. (Arrows indicate colonies resembling the "bacille gommeux" of Winogradsky, 1926.)

Fig. 3.—*Azotobacter*-like organisms, small type, from drop-film; soil No. 8 + glucose, inc. 4 d. 28-30°C. after 2nd addition of glucose.

Fig. 4.—Ditto, big type; from soil No. 10 + glucose and sodium phosphate, inc. 4 d. 28-30°C. after 1st addition.

Fig. 5.—Ditto, very small type; soil No. 32 + filter paper and Ca-lactate, inc. 7 d. 28-30°C.

Fig. 6.—*Azotobacter* from surface colony, soil No. 31 + 33 + wheat straw and calcium carbonate, high moisture content, inc. 3 d. 28-30°C.

Fig. 7.—Clostridia; soil No. 21 + glucose, anaerobic, inc. 7 d. 28-30°C.

Fig. 8.—Blue-green algae; impression preparation from surface of soil No. 8, inc. 90 d. in daylight.

Fig. 9.—Nitrogen-fixing blue-green algae (*Anabaena* sp.?), from culture in mineral solution, inc. 8 weeks in daylight.

Staining: Figs. 3-6, rose bengale; Fig. 7, Gram plus rose bengale; Fig. 8, erythrosine; Fig. 9, unstained.

Magnification: Figs. 3-8, × 625; Fig. 9, × 290.

STUDIES IN APPLIED ECOLOGY. I.

A STATISTICAL ANALYSIS OF REGENERATION FOLLOWING PROTECTION FROM GRAZING.

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(Plates ii–iii; one Text-figure.)

[Read 24th April, 1940.]

Introduction.

Ecology is concerned with the interaction of organism and environment. The common approach to ecological problems is to regard the organism as the dependent and the environment as the independent variable; this approach has led to some understanding of the effect of environment upon plant and animal communities.

Some eighty-five per cent. of the area of New South Wales is under occupation. The effect on the vegetation of such changes in the habitat as man can make is therefore of great importance. In the United States the technique of the ecologist has profitably been applied to problems of land utilization; a similar opportunity to apply ecological technique exists here. The present paper initiates a series of studies in the effects of deliberate changes in the environment upon vegetation.

For some years the country surrounding Broken Hill, New South Wales, has been very badly eroded as a result of timber cutting and heavy grazing by rabbits, goats and stock (Morris, 1939). In an endeavour to protect their new buildings from sand-drift, the management of the Zinc Corporation at Broken Hill fenced, in June–August 1936, about 22 acres on the south-west side of their works. After a few months, during which there were good falls of rain, the protection of this area led to the appearance of many grasses and native shrubs, although it had previously been practically bare. The contrast between the fenced area (now known as the Albert Morris Park) and the surrounding country was so marked that Mr. Albert Morris, at whose suggestion the area had been fenced, found support for a proposal he had advocated for many years: to arrest sand-drift by fencing a wide area round the outskirts of the town. He believed that fencing, by the exclusion of stock and rabbits, would permit the regeneration of the natural plant-cover. With the financial help of the North Broken Hill and Broken Hill South Mining Companies, Mr. A. J. Keast, manager of the Zinc Corporation, fenced about 3·5 square miles of country. The enclosed area lies as a semi-circle of nine paddocks on the southern and western outskirts of the town. The fences are of iron posts and 1·5-inch rabbit-proof netting and were erected during the period from July 1937 to February 1938. In March 1939 an additional area was fenced at the expense of the Government of New South Wales.

The effect of fencing is most beneficial. Areas which previously were sparsely-populated sandy wastes are now occupied by a good cover of grasses and

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native shrubs. Consequently the amount of dust on windy days and the drifting of sand have been reduced. Residents on the outskirts of the town are no longer forced to abandon their homes.

The Albert Morris Park, which is the property of the Zinc Corporation, is irrigated and has been extensively planted with *Atriplex nummularium* and *Eucalyptus* spp., especially *E. camaldulensis*. The other fenced reserves, formerly used by the townspeople for grazing stock, have with one exception not been treated or planted in any way.

With the exception of the work carried out at Koonamore, South Australia, no ecological study has been made in Australian arid country of regeneration of vegetation protected from grazing. The Koonamore studies (Osborn, 1925; Osborn, Wood and Paltridge, 1931, 1932, 1935; Wood, 1936) deal mainly with the regeneration of individual species. In addition the rainfall records at Broken Hill and Koonamore during the period of enclosure are markedly different. Impoverishment of land by wind erosion following overstocking is serious in western New South Wales. Accordingly there is need to study the nature and rate of regeneration in this country. It is not sufficient to know merely that a cover of vegetation is re-established. One needs also to know the names of the more effective colonizing species, and the resistance of the colonizers to drought and competition. From such information as this it should be possible to recommend the propagation of certain species to combat wind erosion, and to foretell the results of fencing as a measure for the control of wind erosion in arid pastoral country.

Description of the Vegetation.

Red sandy plains with scattered rock outcrops and a few sandhills compose the physiography of the reserves. The flora of the enclosed areas and the surrounding commons is predominantly herbaceous (Table i).

The country in the vicinity of Broken Hill is occupied on the plains by communities of *Atriplex* and *Kochia*, frequently admixed with grasses, and on the rocky hills by shrub communities of *Acacia aneura* (mulga) and *Eremophila* (Collins, 1923, 1924). For many miles outside the town the salt-bushes have been almost entirely eaten out, and most species are slow to regenerate. A few plants only of *Atriplex nummularium* (old man saltbush) and only local patches of mulga were recorded in the reserves. The fenced reserves have in all cases already reverted to mixed grassland, in which *Stipa variabilis* is the dominant (Plate iii, fig. 1). Small shrubs of *Cassia* spp., and bushes of *Bassia*, *Kochia* and *Atriplex* are scattered throughout the community. The ground cover is formed by *Schismus*, *Enneapogon*, prostrate species of *Eragrostis*, and by local patches of *Tetragonia* and species of *Zygophyllum* (Plate iii, fig. 2). *Lotus* and *Convolvulus* are notable ground creepers. Shrubs (up to 1–5 metres in height) of *Solanum Sturtianum* and *Sida virgata* occupy the low rocky hills.

In normal seasons the unfenced commons are sandy wastes with a scattered assemblage of weeds, most of them annuals. The time of the present survey (August 1939) was said to be the best season for 27 years. There was on the unfenced ground a fairly good cover of *Malva*, *Tetragonia*, and *Zygophyllum*, with interspersed bare patches varying in extent according to the amount of grazing. Grasses were present, sometimes in large numbers; but individually they were so poorly developed that they did not contribute to the physiognomic character of the community. *Argemone mexicana* and *Salsola Kali* form extensive local societies.

TABLE I.

List of species († = introduced species) recorded in a reconnaissance survey of the Reserves in August 1939. Many of these occur only very infrequently; those of frequent occurrence were recorded by quantitative methods (Table v).

In column 2, the duration of the life-cycles of the species is indicated for the Broken Hill District. A = Annual, B = Biennial, P = Perennial.

In column 3 the degree of palatability is indicated: u, unpalatable; nvp, not very palatable; sp, slightly palatable; mp, moderately palatable; p, palatable; p‡, palatable when young before spiny fruits occur; vp, very palatable; y, in young stages (e.g. p.y, sp.y).

The absence (–) or presence (×) of the species in the adjacent commons is recorded in column 4.

Species.	2	3	4 Occurrence in Commons.	Species.	2	3	4 Occurrence in Commons.
Gramineae							
Aristida arenaria Gaud. ..	P	nvp	–	*B. divaricata* F. Muell. ..	P	p‡	–
[1]†*Avena fatua* L.	A	p	–	*B. eriacantha* R. H. Anderson	P	p‡	–
Chloris acicularis Lindl. ..	P	p	–	*B. lanicuspis* F. Muell. ..	P	p‡	–
†*Cynodon dactylon* Richard	P	p	×	*B. obliquicuspis* R. H.			
Danthonia sp., aff. *semiannularis*	P	vp	×	Anderson	P	p‡	–
Enneapogon sp.	P	vp	×	*B. paradoxa* F. Muell. ..	P	p‡	–
†*Eragrostis Barrelieri* Daveau	A	mp	×	*B. patenticuspis* R. H.			
E. Dielsii Pilger	P	p	×	Anderson	P	p‡	–
E. setifolia Nees	P	p	–	*B. sclerolaenoides* F. Muell.	A	p‡	–
†*Hordeum leporinum* Link.	A	p.y	–	*B. uniflora* F. Muell ..	P	p‡	–
Trisetum pumilum Kunth.	A	mp	–	*Chenopodium carinatum*			
Neurachne Mitchelliana				R. Br.	A	p	×
Nees	P	p	–	*C. murale* L.	A	mp	×
†*Phalaris canariensis* L. ..	A	p	–	*Enchylaena tomentosa* R. Br.	P	mp	–
†*Schismus barbatus* Thell. ..	A	mp	×	*Kochia appressa* Benth. ..	P	mp	–
Stipa variabilis Hughes ..	P	mp	×	*K. aphylla* R. Br. ..	P	mp	–
[1]†*Triticum sativum* Lamarck	A	p	–	*K. brevifolia* R. Br. ..	P	mp	–
Liliaceae				*K. Georgei* Diels.	P	mp	–
Anguillaria dioica R.Br.	P	nvp	–	*K. pyramidata* Benth. ..	P	mp	–
†*Asphodelus fistulosus* L. ..	P	nvp	–	*K. sedifolia* F. Muell. ..	P	p	–
Polygonaceae				*K. tomentosa* F. Muell. ..	P	mp	–
†*Emex australis* Steinheil ..	A	nvp	×	*Rhagodia spinescens* R. Br.	P	p	–
†*Rumex vesicarius* L. ..	A	u	–	*Salsola Kali* Linn. ..	A	sp.y	×
†*Polygonum aviculare* L. ..	A	p	×	*S. Kali* var. *strobolifera*			
Chenopodiaceae				Benth.	A	sp.y	×
Atriplex angulatum Benth.	A	p	–	Amarantaceae			
A. campanulatum Benth.	A	p	–	*Trichinium alopecuroideum*			
A. conduplicatum F. Muell.	A	p	–	Lindl.	A	mp	–
A. halimoides Lindl. ..	A	p	–	*T. obovatum* Gaud. ..	P	mp	–
A. Muelleri Benth. ..	A	p	×	*T. spathulatum* R. Br. ..	P	mp	–
A. nummularium Lindl. ..	P	p	–	Aizoaceae			
A. spongiosum F. Muell. ..	A	p	–	*Tetragonia expansa* Murr.	A	p	×
A. stipitatum Benth. ..	P	p	×	Portulacaceae			
A. vesicarium Heward ..	P	p	–	*Calandrinia pusilla* Lindl.	A	p	–
Babbagia acroptera F.Muell.				*Portulaca oleracea* Linn. ..	A	p	×
& Tate	A	sp	–	Caryophyllaceae			
Bassia brachyptera R. H.				*Polycarpaea corymbosa* Lam.	A	sp	–
Anderson	P	p‡	–	*Spergularia rubra* Camb.	A	sp	–
B. convexula R. H. Anderson	P	p‡	–	Papaveraceae			
				†*Argemone mexicana* L. ..	A	u	×

[1] Occurs only in drains where fruit has been washed from the town.

†*Glaucium corniculatum* L.	A	—	—
Cruciferae			
Blennodia lasiocarpa F. Muell.	A	p	×
B. trisecta Benth.	P ?	p	×
†*Diplotaxis muralis* DC. ..	A or B	nvp	—
Lepidium papillosum F. Muell.	A	p	×
Stenopetalum lineare R. Br.	A	p	×
†*Sisymbrium officinale* L. ..	A	mp	✓
†*Rapistrum rugosum* All. ..	A	sp	×
Leguminosae			
Acacia aneura F. Muell.	P	p	—
A. tetragonophylla F. Muell.	P	sp	—
A. Victoriae F. Muell. ..	P	sp	—
Cassia artemisioides Gaud.	P	mp	—
C. eremophila Cunn. ..	P	mp	—
C. eremophila var. *platypoda* Benth.	P	mp	—
C. Sturtii R. Br.	P	mp	—
Clianthus Dampieri A. Cunn.	A or B	p	—
[2]*Lotus australis* var. *pubescens* Benth. ..	A	mp	×
Swainsona fissimontana J. M. Black	A	sp ?	—
S. stipularis F. Muell. ..	A	sp	—
Trigonella suavissima Lindl.	A	p	—
†*Vicia sativa* L.	A	p	—
Geraniaceae			
†*Erodium Botrys* Bertol. ..	A	p	—
E. cygnorum Nees ..	A	p	×
†*E. cicutarium* L'Hér. ..	A	p	—
Zygophyllaceae			
Zygophyllum ammophilum F. Muell.	A	nvp	×
Z. crenatum F. Muell. ..	A	nvp	×
Z. iodocarpum F. Muell. ..	A	nvp	×
Euphorbiaceae			
[2]*Euphorbia Drummondii* Boiss.	A	mp	×
Sapindaceae			
Dodonaea lobulata F. Muell.	P	sp	—
Malvaceae			
Abutilon sp.	P		×
Hibiscus Sturtii Hook. ..	P	sp	—
†*Lavatera plebeia* Sims ..	A	sp	—
†*Malva parviflora* L. ..	A	sp	×
Sida corrugata L.	P or B	sp	×
S. intricata F. Muell. ..	P or B	nvp	×
S. virgata Hook	P	nvp	—
Asclepiadaceae			
Marsdenia australis J. M. Black	P	u	—
Convolvulaceae			
Convolvulus erubescens Sims	P	mp	×
Boraginaceae			
†*Echium plantagineum* L.	A	p	×
†*Heliotropium asperrimum* R.Br.	A	u	—
Lappula concava F. Muell.	A	sp	×
†*Lithospermum arvense* L. ..	A	sp	—
Labiatae			
Prostanthera striatiflora F. Muell.	P	sp	—
Solanaceae			
Lycium ferocissimum Miers.	P	u	—
[2]*Nicotiana glauca* Graham	P	u	—
[2]*Solanum ellipticum* R. Br.	P	u	—
[2]*S. opacum* L.	A	u	×
[3]*S. petrophilum* F. Muell. ..	P	u	—
[2]*S. Sturtianum* F. Muell. ..	P	u	×
Myoporaceae			
Myoporum montanum R. Br.	A	mp	×
Eremophila serrulata Druce	P	mp	—
Cucurbitaceae			
†*Cucumis myriocarpus* Naudin	A	nvp	×
†*Citrullus vulgaris* Schrad.	A	nvp	×
Campanulaceae			
Isotoma petraea F. Muell...	P	nvp	—
Wahlenbergia gracilis DC.	P	mp	—
Goodeniaceae			
Goodenia glauca F. Muell...	P	sp	—
Compositae			
Angianthus Burkittii J. M. Black	A	sp	—
Brachycome ciliaris Less.	A	mp	—
B. pachyptera Turcz. ..	A	mp	—
Craspedia Chrysantha Benth.	A	mp	—
Calotis cymbacantha F. Muell.	A	mp	×
†*Carthamus lanatus* L. ..	A	mp	×
†*Centaurea melitensis* L. ..	A	p.y	×
Cryptostemma calendulaceum R. Br.	A	sp	—
Gnaphalodes uliginosum A. Gray	A	sp	✓
Helipterum albicans DC...	A	sp	—
H. corymbiflorum Schlecht.	A	mp	—
H. floribundum DC. ..	A	mp	—
H. microglossum Tate ..	A	sp	✓
H. moschatum Benth. ..	A	sp	—
H. polygalifolium DC. ..	A	sp	—
H. pygmaeum Benth. ..	A	sp	—
Inula graveolens Desf. ..	A	sp	—
Ixiolaena leptolepis Benth.	P	mp	—
Podolepis canescens A. Cunn.	A	sp	—
Senecio brachyglossus F. Muell.	A	mp	—
S. Gregorii F. Muell. ..	A	mp	—
†*Sonchus oleraceus* L. ..	A	vp	×
Vittadinia australis A. Rich.	P	sp	—

[2] Poisonous.

[3] Poisonous to sheep.

Quantitative Analysis.

It is clear from Plate ii, figures 1 and 2, that even in so short a time as two years, fencing the land has restored the vegetation. In order to follow in greater detail the history of recolonization a permanent quadrat of 50 square metres was laid out in one of the fenced reserves (regeneration reserve no. 4, enclosed in September 1937). The position and approximate size of every individual in this quadrat has been entered on a chart. Mrs. M. Morris, of the Zinc Corporation, who directs the regeneration work in the Albert Morris Park, has kindly undertaken to make records of the changes in this quadrat from time to time, in order to determine the effects of fluctuations of climate upon the population.

That there has been a change of vegetation following fencing is too evident to need analysis; but there are certain features of the change which can be disclosed only by the use of quantitative methods. Has, for instance, fencing increased the richness of the flora (number of species) or merely the density (number of individuals per unit area)? Is the change due to a profusion of annuals or to the spread of perennial plants? Is more ground covered with vegetation or is the vegetation merely taller? Can one obtain some precise way of measuring the rate of colonization? Is the permanent quadrat an adequate sample of the whole community, i.e. can conclusions drawn from the quadrat be extended to the whole area? What is the incidence of species with increase in area? In order to answer such questions as these it is necessary to study the dispersion of the various species in the community.

The basic assumption in describing vegetation from a sample area is that the environment and vegetation are uniform, i.e. that the species are as a whole randomly distributed. This randomness will not be apparent until a certain limiting area is reached; the size of this limiting area depends upon the coarseness of the mosaic of species which compose the community. The coarser the mosaic, i.e. the less frequently any species recurs in the community, the larger must any permanent quadrat be if it is to represent the whole. The ecologist is now supplied with statistical methods which enable him to test the assumption of randomness in communities and in species. The tests applied in the present study fall into two categories: (i) the relation between species and area, and (ii) the density and distribution of individual species in fenced and unfenced areas.

Method of Sampling.—Before entering upon a statistical analysis of a plant community it is necessary to decide upon the shape and size of the samples to be taken.

(*a*) *Shape of sample areas.*—It has been customary to sample vegetation by means of square quadrats. In dense communities there is often difficulty in laying such quadrats on the ground; in the fenced areas at Broken Hill this difficulty would have been considerable. Accordingly in this work the vegetation was sampled by means of rectangular strips of 1·05 and 1·50 square metres. The sampling was carried out simply by laying a string seven or ten metres in length at random over the community, and counting all the plants within 15 centimetres on one side of this string. The use of rectangular strips in place of square quadrats has the additional advantage that the variance of samples from strips is less than that of samples from squares of the same area. A strip therefore yields more information

than a square. Clapham (1932) found that the estimated variance of species counts from square and rectangular plots was as follows:

Shape of plot	Estimated variance
Square metre quadrats	400·80
Strips 4m. × 0·25m.	219·77

(*b*) *Size of sample strips.*—It has been shown experimentally (Ashby, 1935) that the relation between the chance of finding a randomly distributed species in a quadrat and the density of the species is not linear but logarithmic, and is expressed by the equation:

$$p = 1 - e^{-kx}$$

where p = the probability of occurrence of the species in a quadrat of size k, and x = the density in number of individuals per unit area. The variance of x increases rapidly for high values of p, so that a large quadrat laid a few times will not give such an accurate measure of density as a small quadrat laid many times. There is, moreover, a lower limit to the size of a quadrat: it must not be so small that the size of the plants becomes an appreciable fraction of the quadrat size. The size of the quadrat must lie within these two extremes. The simplest method of choosing the appropriate size is to find by preliminary trial an area such that few species occur with a frequency exceeding 80 per cent. Under these conditions (Ashby, 1935, p. 787) most species will have a frequency of 20 per cent. or less. This is the optimum condition for sampling a community. In the present instance it was found that a 1·50 metre sample (10m. × 0·15m.) gave the distributions of species in the different communities shown in Table ii. These distributions conform with the above requirements; this size was accordingly chosen. The sampling was carried out in two fenced reserves and in the two adjacent unfenced commons. The areas chosen were the west reserve (regeneration reserve no. 9) enclosed in December 1937, and the south reserve (racecourse extension to reserve no. 1) enclosed in February 1938. Fifty random samples were taken (i.e. 75 square metres) in the fenced west reserve and the adjacent unfenced common, forty samples (60 square metres) in the fenced south reserve, and 39 samples (58·5 square metres) in the unfenced south common.

TABLE II.

Number of species in frequency classes, using a sample area of 1·50 square metres (10m. × 0·15m.).

Frequency Class.	0–20	21–40	41–60	61–80	81–100	Total
West reserve fenced	19	6	3	2	5	35
West common unfenced	19	2	4	2	3	30
South reserve fenced	23	6	3	0	3	35
South common unfenced	17	5	4	1	5	32

SPECIES-AREA CURVES.—It is inadmissible to draw conclusions from samples of the fenced and unfenced areas unless it can be shown that the distribution of species in the community is approximately at random. A test of random distribution in the fenced and unfenced areas was made from the species-area curves, obtained from counts of the number of species occurring in sample strips of different sizes. The larger samples are not composed from a random assortment of the smaller samples, as some workers have done (Arrhenius, 1921), for it has been pointed out (Blackman, 1935) that the method of grouping small samples to make large ones obscures any irregularity in the distribution of species.

Consequently the sampling was done by increasing the size of the original, e.g. 10m. × 0·1m. → 50m. × 0·1m. → 50m. × 0·2m. → 50m. × 1m. → 100m. × 1m. → 100m. × 2m. The data are presented graphically in Figure 1. If the distribution of species is not distorted by local disturbances, but is due to chance, the relation between species and area should approximate to some exponential function, e.g.:

$$n = m\log a + b$$

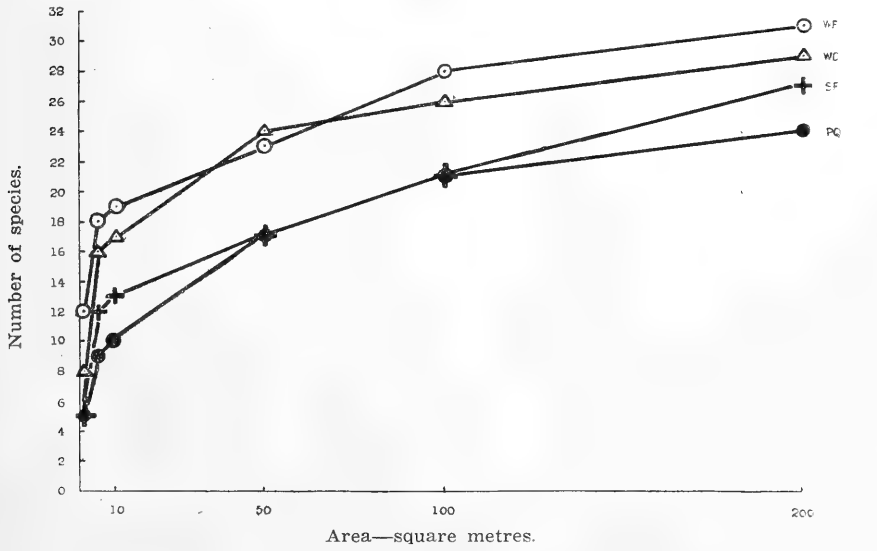
where n = number of species, a = area, b = number of species per unit area, and m is a constant which measures the floristic variety of the community.

An agreement between the observed data and values calculated from this equation would indicate that the community is homogeneous and uniformly distributed. It would then be justifiable to draw conclusions from the sample to the whole; although such a relation as this cannot be extrapolated to very high values of "a" because, as the area is increased, heterogeneity of the environment is bound to increase. The results of the comparison are presented in Table iii.

TABLE III.

Observed (obs.) and calculated (cal.) number of species for four sampled communities, using increasing sample areas.

Area of Sample (sq. m.)	Western Area Unfenced Obs.	Unfenced Cal.	Fenced Obs.	Fenced Cal.	Southern Area Fenced Obs.	Fenced Cal.	Permanent Quadrat Fenced Obs.	Fenced Cal.
1	8	9·0	12	11·6	5	5·0	5	2·6
5	16	15·0	18	17·4	12	10·9	9	8·9
10	17	17·5	19	20·0	13	13·5	10	11·5
50	24	23·6	23	26·0	17	19·5	17	17·7
100	26	26·2	28	28·6	21	22·2	21	20·5
200	29	28·7	31	31·1	27	24·8	24	23·1



Text-figure 1.

Number of species plotted against area; ordinates number of species, abscissae area in square metres.

WF, West fenced; WC, West control (unfenced); SF, South fenced; PQ, Permanent quadrat (fenced).

From these figures it seems clear that there is no striking heterogeneity in the communities. On the assumption of random distribution a good agreement is obtained between calculated and observed values. It may safely be assumed therefore that a sample in one part of the community will be an adequate expression of the whole community.

An interesting feature of secondary importance appears from this test. It should be possible, since the equation fits the data fairly well, to predict the total number of species within a known area of each regeneration reserve. This has been done for three of the reserves on which one of us (I.M.P.) had made fairly complete lists of species. The agreement between the number of species found on the observed area (roughly estimated in acres) and the calculated number is shown in Table iv. The probability in favour of this agreement (calculated from a value of $\chi^2 = 1{\cdot}012$) is over 60 per cent.

TABLE IV.

Observed number of species on three of the areas compared with the numbers calculated from the equation $n = m\log a + b$.

Situation	Approximate Area (acres)	Number of Species Obs.	Cal.	Difference
West, unfenced	3	37	43·4	−6·4
West, fenced	8	50	50·4	−0·4
South, fenced	8	47	44·0	3·0

This assurance that the communities are homogeneous is a most important pre-requisite for detailed ecological research. A great many of the ecological analyses published in the literature are invalidated because this precaution was not taken, despite the fact that the communities studied were obviously not homogeneous. The analysis of species-area curves emphasizes also the limitations of the permanent quadrat. It is not practicable to make such a quadrat too large, and it is well to know that the permanent quadrat chosen contains about 35 per cent. of the total flora of the area, and that even one sample strip of 1·50 square metres contains about 20 per cent. of the species.

DENSITY OF INDIVIDUAL SPECIES.—Table v summarizes the density of the species as recorded from sample strips in the fenced and adjacent unfenced areas. Table vi summarizes the approximate total number of species in all reserves and adjacent commons, and in the west and south reserves. General observations, not evident from the quantitative analysis, on type of growth, cover and height of vegetation, are summarized in Table vii.

From an inspection of Tables v and vi, the following conclusions may be drawn as to the effect of a brief period of protection from grazing:

(i). Table vi records the species counts from inspection of the areas, not from formal sampling; but it shows that after approximately two years, fencing has been followed by a considerable increase in the number of perennial *species*. As pointed out previously, some of these species are only of rare occurrence. From the same table, it appears that there is a greater variety of perennial species in the west than in the south reserve. The same conclusions may be drawn from Table v, even though only one-third of the number of species is listed. The differential effect of fencing can be attributed only to a chance distribution of seed or to a slight variation in the environment. Table vi also shows that fencing, by

TABLE V.

Density of the species as recorded from sample strips in two fenced and adjacent unfenced areas. The results are expressed to the nearest whole number per 100 square metres, calculated from counts of the number of individuals on 75 m² (western areas), 60 m² (south fenced) and 58·5 m² (south unfenced). Figures printed in *italics* represent densities which are randomly distributed (P>0·05).

Localities: W.F. = West fenced (reserve); W.C. = West control (unfenced); S.F. = South fenced (reserve); S.C. = South control (unfenced).

Perennial Species	Densities in various localities				Annual Species	Densities in various localities			
	W.F.	W.C.	S.F.	S.C.		W.F.	W.C.	S.F.	S.C.
Stipa variabilis ..	958	175	1112	1193	*Eragrostis Barrelieri* ..	2465	1540	390	625
Eragrostis Dielsii ..	*51*	*60*	577	468	*Schismus barbatus* ..	372	97	—	*22*
Enneapogon sp. ..	157	*12*	—	3	*Tetragonia expansa* ..	447	1011	218	786
Danthonia sp. ..	64	*11*	3	2	*Argemone mexicana* ..	*23*	205	20	20
Sida intricata ..	23	*7*	15	12	*Centaurea melitensis* ..	421	64	2	5
S. corrugata	*132*	*22*	*15*	87	*Salsola Kali*	130	1	*15*	5
Convolvulus erubescens	59	*23*	45	*26*	*Sonchus oleraceus* ..	*8*	*7*	2	*14*
Cassia eremophila ..	13	1	3	3	*Malva parviflora* ..	47	299	*12*	576
Bassia uniflora ..	31	—	—	—	*Lotus australis* ..	*58*	130	37	39
B. patenticuspis ..	4	4	—	—	*Zygophyllum crenatum*	—	—	110	183
Cassia artemisioides ..	4	—	—	—	*Z. ammophilum* ..	—	—	73	22
Atriplex stipitatum	16	—	2	*14*	*Z. iodocarpum* ..	—	—	183	58
Blennodia trisecta ..	—	—	45	*19*	*Echium plantagineum*	—	—	13	15
Cynodon Dactylon ..	—	4	2	—	*Cucumis myriocarpus*	1	—	2	10
Goodenia glauca ..	4	—	—	—	*Citrullus vulgaris* ..	—	—	3	10
Solanum Sturtianum ..	7	—	—	—	*Sisymbrium officinale* ..	—	6	5	10
Trichinium obovatum ..	1	—	—	—	*Lepidium papillosum*	—	—	33	17
Abutilon sp.	1	—	—	2	*Erodium Botrys* ..	7	9	40	—
Marsdenia australis ..	1	—	—	—	*E. cygnorum*	—	—	5	—
					E. cicutarium ..	—	—	2	—
					Calotis cymbacantha	1	4	2	22
					Chenopodium carinatum	4	7	—	—
					Lappula concava ..	—	1	2	2
					Euphorbia Drummondii	4	3	—	—
					Swainsona fissimontana	4	—	—	—
					Clianthus Dampieri ..	7	—	—	—
					Gnaphalodes uliginosum	—	3	—	—
					Calandrinia pusilla ..	—	—	2	—
					Atriplex spongiosum ..	—	—	3	—
					Blennodia lasiocarpa	—	—	3	2
					Carthamus lanatus ..	1	1	—	—
					Rumex vesicarius ..	1	—	—	—
					Helipterum microglossum	—	3	—	—
					Trigonella suavissima	—	—	—	1
					Cryptostemma calendulacea	—	1	—	—
					Trisetum pumilum ..	—	1	—	—
Total number species	17	10	10	11		18	20	25	21
Total number individuals	1526	319	1819	1829		4001	3393	1176	2444

Grand Totals

	W.F.	W.C.	S.F.	S.C.
Species	35	30	35	32
Individuals	5527	3712	2995	4273

TABLE VI.

Approximate total number of annual and perennial species in all the reserves and adjacent commons, and in the west and south reserves. Data obtained from reconnaissance surveys.

		Number of Species		
		Perennial	Annual	Total
All reserves	Compiled from Table I	65	78	143
All adjacent commons	Compiled from Table I	12	35	47
West reserve	Compiled from Table I	43	53	96
South reserve	Compiled from Table I	30	48	78

TABLE VII.

Comparison of features of the vegetation in the reserves and adjacent grazed commons.

	Fenced Reserves.	Unfenced Commons
Height of vegetation	About 60 cm.	Ground flora 10 cm. with irregularly scattered weeds up to 30 cm.
Cover	In most of the reserves the perennial vegetation forms a fairly continuous cover.	Considerable areas of bare ground.
Grasses	(i) Mature plants. (ii) Flourishing. (iii) Firmly rooted. (iv) *Stipa* tufts up to 75 cm. (See Pl. iii, figs. 1, 3.)	(i) No well-developed plants. (ii) Dying off in young and early-mature stages. (iii) Often partially uprooted by grazing stock. (iv) Prostrate. (See Pl. iii, fig. 4.)
Weeds (undesirable species)	(i) Mostly small plants and seedlings. (ii) *Malva*: limited in occurrence by competition with *Stipa* tufts.	(i) Mostly mature. (ii) *Malva*: extensive spreading colonies, overrunning grasses.
Sand-binders	*Sida intricata* and *S. corrugata* occur as mature spreading plants holding extensive mounds of sand.	*Sida* spp. not evident as sand-binders. Occur mostly as seedlings.

protecting seed, has increased the variety of annual species, but obviously this is of much less significance.

(ii). Fencing has a marked effect on the mean density of individuals per unit area. In the west reserve, which has been fenced for twenty months, protection has greatly increased the number of individual perennial *plants*. In the south reserve, which has been fenced for 18 months, there has been no change. Another notable feature is that the total number of perennial plants in the west reserve is about 15 per cent. lower than that in the south reserve. These differences are mainly due to differential conditions of the two areas before fencing. The western area was much more heavily grazed than the southern area because it was near several dairies. In addition there were, on the west reserve, a large number of tracks and bare areas on which the top soil was worn and washed away. On the other hand, the south reserve formerly used to be the old racecourse which was not open to grazing until a few years ago. It is also situated to the windward of and immediately adjacent to the oldest block in the regeneration reserve, and therefore it had an initial advantage with regard to availability of seed. These

differential environmental conditions are reflected in the physiognomy of the vegetation of the two reserves. The south reserve appears to be adequately covered while in the west reserve there are many bare patches. In the south reserve the individual plants are better developed, e.g. the percentage of mature *Stipa* plants in the south is 56 compared with 40 in the west. Thus, although it has actually been enclosed for a shorter period, the south reserve is far ahead of the west from the point of view of succession. The same conditions with regard to differential grazing still applied on the unfenced commons at the time of the survey. The west common was heavily grazed and was characterized by large areas of bare ground, whereas the south common was fairly well covered. These differences are strikingly reflected in the mean density of perennials in the two commons. Marked differences between the density of perennials in the south fenced and unfenced areas are not to be expected because of the light grazing. The main difference between the perennial flora in these areas is in the height of the grasses (see Pl. ii, fig. 1). Thus the effect of protection from grazing on the perennial flora is determined by the condition of the land before fencing. Fencing may increase the number of individuals in bare areas or it may merely improve the growth of individuals already present.

The effect of fencing on the annual flora is of much less importance, partly because of the limited period during which annuals are effective sand-binders and partly because their numbers vary considerably with the seasons. However, the results are interesting. Both areas in the south have relatively few annuals because of competition with perennials. This is very marked in the south reserve where the perennial grasses are so well developed that there is little space open to annual invaders. The west reserve and common have a much larger annual population because of their extensive bare areas; the west reserve has the larger mean density of annuals because of protection.

(iii). Protection from grazing affects the density of individual species in general by decreasing the number of so-called weeds or undesirable species, and by increasing the number of perennials, particularly of palatable species. In the elucidation of Table v the following suggestions are made as to the effect of fencing on the more important species:

Perennial Species.

Grasses.

(*a*). *Stipa variabilis**: In the west area, protection has markedly increased the density, but there is no significant difference in the south. This may be explained by differential grazing as discussed above, and also by the fact that the position of the south reserve is such that the prevailing westerly winds carry fruits directly on to the unfenced common. The west unfenced area is not so favourably situated.

(*b*). *Eragrostis Dielsii*: This species appears to be independent of grazing. It has a prostrate habit of growth and is therefore grazed mainly by sheep, whereas this area is grazed mainly by cattle. The greater density of *Stipa* and *Eragrostis Dielsii* in the south is probably due to the fact that the south reserve is to the windward of the oldest reserve.

(*c*). *Enneapogon* and *Danthonia*: Protection has increased the density only in the west. These species are very palatable and were almost eaten out. They do not seed abundantly, and *Danthonia* spp. often have a low percentage germina-

* This grass is believed to be the same as that discussed by Osborn, Wood, and Paltridge (1931). The nomenclature of this species is still under revision.

tion. The differential establishment is probably due to availability of seed; when seed is available, there is every reason to suppose that these grasses will become established in the south reserve.

Erect shrubs or undershrubs.

(*a*). *Sida corrugata* and *S. intricata*: These species appear to be independent of grazing. The high densities obtained in the west reserve for *S. corrugata* were due mainly to seedlings.

(*b*). *Bassia uniflora*: Palatable when young; fencing increases numbers in west reserve.

(*c*). *Cassia eremophila*: A marked increase in the fenced western reserve, where it added a distinctive character to the community. *Cassia* spp. were plentiful before grazing. At Koonamore, *Cassia eremophila* was recorded as regenerating rapidly after rains.

(*d*). *Atriplex stipitatum*: According to Wood (1936) this is the least palatable of the perennial species of *Atriplex* owing to a bitter principle which it contains. Its relative high density in the south common is an indication of the light grazing in this locality, and also of the relative abundance of grasses. At Koonamore, this species was noted for its free-seeding, ready germination and rapid regeneration; it is therefore significant that at Broken Hill it was the first of the perennial saltbushes to reappear in considerable numbers.

Creepers.

(*a*). *Convolvulus erubescens*: In both areas fencing has increased the density. This species is palatable in mixed grazing.

Annual Species.

As with all annuals, density per unit area is dependent on a complex of factors such as availability of seed and space and on ability to withstand competition. Since the south and west areas are separated by several miles, the available seed may vary in the two areas, and, as has already been mentioned, the proportion of bare ground for colonization is much greater in the west than in the south reserve. In addition, the following points explain some of the differences in distribution of annuals:

Grasses.

(*a*). *Eragrostis Barrelieri*: This species is eaten, but it is probably only moderately palatable. Although it is a free-seeding grass, its density is increased by fencing only when competition is not severe. The highest densities are in the western section where there is least competition.

(*b*). *Schismus barbatus*: Probably a fairly palatable species. Its behaviour is much the same as *Eragrostis Barrelieri*, except that it is not so widespread. Its absence from the south regeneration reserve may be attributed to competition or to absence of seed.

Prostrate spreading herbs.

(*a*). *Tetragonia expansa*: Said to be good fodder, but at the time of the survey did not appear to be eaten by stock, probably because of the relative abundance of more palatable species. In both cases fencing, by increasing competition, decreases the density.

(*b*). *Zygophyllum* spp.: Eaten by stock, but said to be not very palatable. Absence from southern area probably correlated with inefficient seed dispersal (succulent fruits). Fencing has increased only *Z. ammophilum* and *Z. iodocarpum*

and, although no information is available, this rather suggests that these two species may be more palatable.

(*c*). *Clianthus Dampieri*: (May be a biennial in good seasons.) A very palatable species, which had disappeared from this area more than 30 years ago. Its fruits are known to be highly resistant and long lived; germination must have been from very old seed. Protection will therefore increase this species.

(*d*). *Lotus australis*: Reports differ, but it is said to be a poisonous plant containing hydrocyanic acid; it may be only undesirable in certain combinations of feed. Fencing decreases the density in the west reserve by competition. In the southern area in this particular season, there is competition both inside and outside the fences. Apparently this species is unable to endure much competition, even in the absence of a vigorous growth of grasses (see also *Argemone*, *Centaurea*, *Salsola*).

Herbs or undershrubs, usually erect.

(*a*). *Malva parviflora*: This is usually an erect plant, but at Broken Hill at the time of the survey it was diffuse and spreading. It is either unpalatable or only slightly palatable and in both reserves its density has been markedly decreased by competition.

(*b*). *Argemone mexicana*: Very unpalatable and on the whole undesirable, although it has been recorded as effectively retaining wind-blown sand.

(*c*). *Centaurea melitensis*: Palatable only in young stages and regarded as a pest.

(*d*). *Salsola Kali*: Fairly good fodder when young and camels eat it even when dry. It is an effective sand-retainer during the spring season, but its habit of piling against fences makes it undesirable. *Argemone* reacts in the same way as *Lotus*. Both are unable to stand competition; their highest density is in the unfenced western common where there is least competition. On the other hand, *Centaurea* and *Salsola* are at first increased by protection (west reserve), but are crowded out when competition is more severe (south reserve). The fact that *Salsola*, *Centaurea*, *Lotus* and *Argemone* have approximately the same densities in the south fenced and unfenced areas indicates that these particular species are kept in control equally well by competition with grasses (fenced area) or with robust spreading types such as *Malva* and *Tetragonia* (unfenced area). This effect is not apparent under heavy grazing or in bad seasons; both factors decrease mean density of cover and consequently competition.

Distribution of Individual Species.—The distribution of individual species in the areas examined must be either random, or over- or under-dispersed. If distribution is random it is possible to estimate accurately changes in density over wide areas by rapid sampling methods, for the relation between the chance of finding 0, 1, 2, ... n plants in a sample strip and the mean density of the species is given by the terms of a Poisson distribution:

$$\frac{1}{e^{kx}}\left(1,\ kx,\ \frac{(kx)^2}{2!},\ \ldots\ldots\ \frac{(kx)^n}{n!}\right)$$

where k is the area of the strip as a fraction of the unit area, and x is the mean number of individuals per unit area. Agreement with the hypothesis of random dispersion may be tested by the application of the χ^2 function. If there is random dispersion the ecologist (and the agrostologist) has a most valuable tool for studying changes in plant populations (Svedberg, 1922; Blackman, 1935; Clapham, 1936; Ashby, 1936). In the few instances previously studied it has been found that many species are not randomly distributed, but are over-dispersed (i.e.

aggregated) so that proximity to another member of the same species is the more favourable site for colonization. This aggregation is due to one or more of three causes: the stage of colonization of the species, its mode of reproduction, or soil heterogeneity. Under intense competition, on the other hand, species may be over-dispersed, so that the more favourable sites are those removed from other individuals. A knowledge of the type of dispersal of a species enables the ecologist to draw conclusions as to its manner and rate of colonization in relation to the environment. When the densities set out in Table v were recorded from the sample strips, information was obtained as to the number of strips with 0, 1, 2, etc. individuals of each species. From these data it is possible to determine how many of the species are randomly distributed, and how many show aggregation or over-dispersion. The data are too extensive to reproduce in full, but in column 3 of Table ix the agreements with Poisson distributions are recorded for all random species as probabilities from the table of χ^2. It may be assumed that departure from randomness is not significant unless the values of P (the probability) are less than 0·05. A few examples showing the degree of agreement with Poisson distributions are given in Table viii.

TABLE VIII.

Observed and calculated number of throws of sample strip containing 0, 1, 2, ... individuals. Total 100 throws. Calculations expressed to the nearest whole number.

Species	Locality	—	0	1	2	3	4	5	6
Enneapogon sp. ..	W.C.	obs.	84	14	2				
P = 0·70		cal.	83	15	2				
Schismus barbatus ..	S.C.	obs.	72	23	5				
P = 0·60		cal.	72	24	4				
Sida corrugata ..	W.F.	obs.	26	30	30	8	4	0	2
P = 0·55		cal.	24	34	24	11	5	1	1
Sida intricata ..	W.F.	obs.	76	22	2				
P = 0·45		cal.	77	20	3				
Sida intricata ..	S.F.	obs.	90	5	3	2			
P = 0·01		cal.	84	14	1·2	0·8			
Danthonia sp. ..	W.F.	obs.	46	32	12	4	0	6	
P = 0·01		cal.	38	37	18	6	1		

It will be observed that agreement among the first four species is tolerably good, and among the last two it is poor. From these data were calculated the probabilities of agreement with the hypothesis of random distribution. These are given with the complete list of species in Tables ix and x. In Table ix it should first of all be observed that in 24 cases departure from the assumption of random distribution (Poisson distribution) is not significant. In these cases the number of *empty* sample strips may be taken as a basis for the calculation of density. Thus, in order to discover any change in the density of *Sida corrugata* in the western reserve it would be unnecessary to count the number of individuals; it would suffice to lay the sample strip randomly over the area and to find the percentage

of strips in which Sida *does not occur*.* Other workers (Blackman, 1935; Clapham, 1936, dealing with data from Steiger, 1930) find that in grassland relatively few species are randomly distributed. It is therefore of some ecological interest to find so many instances of random distribution in what is essentially a grassland community. Singh and Das (1938, 1939) find that most weeds in arable land are randomly distributed. They worked on weeds which colonized land during a short fallow; and it may be that in the present work, as in theirs, the high proportion of randomly distributed species is a symptom of an early stage of colonization, and would disappear as the community became consolidated. Further evidence in favour of this view is given below.

Where distribution is random it should be practicable to replace the laborious counting of plants by the rapid method of percentage absence. This is demonstrated in Table ix by comparing the actual counts of individuals in the several areas with the density calculated (*a*) from the whole of the appropriate Poisson distribution, and (*b*) from the percentage of empty strips alone. For practical purposes it is the agreement between observed density and density calculated from the percentage absence which matters. This agreement is tested by means of the χ^2 distribution. It will be seen that the agreement for all species with a value of $P > 0{\cdot}05$ is good. The densities of species which have values of $P < 0{\cdot}05$ bear, of course, no simple relation to their percentage absence in sample strips.

The data summarized in Table ix contain another noteworthy feature. The same species may be randomly distributed in one area and aggregated in another. *Convolvulus*, for instance, occurs randomly in unfenced areas, and is aggregated in the fenced areas. Other species (*Malva*, *Lotus*) are randomly distributed in one area only, and aggregated in the rest. It is therefore inadmissible to consider the distribution of any species as random "by nature". From a comparison of Tables v and ix, a cause for this inconsistency may be suggested: namely, that normality of distribution seems to disappear with increasing density. The possibility of this has already been mentioned. Table xi, which is composed from the data of Tables v, ix and x, illustrates this point. This table contains the distributions (random or non-random) of all observations of density greater than 5 per 100 square metres, according to three density classes. It is clear from the table that species are randomly distributed only at moderate densities, and that all observations of densities exceeding one individual per square metre (with the exception of *Sida corrugata*) are non-random. This suggestion is supported by the fact that randomness among perennials is about twice as common in the west, which is more sparsely populated (1,845 individuals) than in the south (3,648 individuals).

* Thus the observed density of *Sida* in the west fenced reserve was 99 individuals in 75 square metres. Of 100 throws of the sample strip of 1·50 square metres, 26 were free from *Sida*. Therefore we may say that $e^{-kx} = 26$, $kx = 1{\cdot}35$, $x = 96{\cdot}45$.

TABLE IX.

Comparison of calculated and observed densities of randomly distributed species.

Cal. (*a*) is calculated value from Poisson distribution; Cal. (*b*) is calculated value from the number of empty sample strips.

Localities: W.F. = West fenced (reserve); W.C. = West control (unfenced); S.F. = South fenced (reserve); S.C. = South control (unfenced).

Species.	Locality	P	% Absence	Density (plants per plot)			Obs.−Cal. (*b*)
				Observed	Cal. (*a*)	Cal. (*b*)	
Convolvulus erubescens	W.C.*	0·99	82	17·0	15·0	16·50	0·50
Convolvulus erubescens	S.C.	0·85	67	15·0	14·8	15·62	−0·62
Lotus australis ..	W.F.*	0·99	54	43·0	43·0	43·50	−0·50
Enneapogon sp. ..	W.C.	0·70	84	9·0	9·0	8·75	0·25
Schismus barbatus	S.C.	0·60	72	13·0	12·9	12·87	0·13
Sida corrugata ..	S.F.	0·99	80	9·0	8·8	8·76	0·24
,, ,, ..	W.C.*	0·07	80	16·0	14·2	15·75	0·25
,, ,, ..	W.F.*	0·55	26	99·0	100·0	96·45	2·55
Sida intricata ..	S.C.	0·05	84	7·0	7·4	6·61	0·39
,, ,, ..	W.C.*	0·40	92	5·0	5·7	5·47	−0·47
,, ,, ..	W.F.*	0·45	76	17·0	18·6	18·00	−1·00
Danthonia sp. ..	W.C.	0·25	86	8·0	7·0	7·50	0·50
Atriplex stipitatum	S.C.	0·70	82	8·0	8·2	7·76	0·24
Sonchus oleraceus ..	S.C.	0·99	82	8·0	7·8	7·76	0·24
,, ,, ..	W.F.	0·30	90	6·0	5·0	5·25	0·75
,, ,, ..	W.C.	0·30	90	5·0	5·0	5·25	−0·25
Erodium Botrys ..	W.F.*	0·05	92	7·0	7·1	5·70	1·30
Salsola Kali ..	S.F.	0·06	77	9·0	9·2	10·41	−1·41
Malva parviflora	S.F.	0·25	88	7·0	5·6	5·12	1·88
Blennodia trisecta	S.C.	0·15	79	11·0	10·2	9·36	1·64
Argemone mexicana	W.F.	0·40	74	17·0	17·2	15·00	2·00
Eragrostis Dielsii	W.F.*	0·60	62	38·0	34·2	34·28	3·72
,, ,,	W.C.*	0·30	62	45·0	41·5	34·28	10·72
Zygophyllum iodocarpum ..	S.C.	0·35	46	34·0	32·4	30·42	3·58

* Sample strip 1·05 m²; elsewhere 1·50 m².

χ^2 for n=24−1 : 6·269. P>0·99

TABLE X.

Distribution of species according to their density classes. Figures are percentages of the whole number of observations, excluding all those observations with densities less than five individuals per 100 square metres.

Classes of density (100 m²)	Random distribution			Non-random distribution		
	Perennials	Annuals	Total	Perennials	Annuals	Total
0–50	10·6	9·4	20·0	10·6	27·1	37·7
51–100	2·4	1·2	3·5	3·5	4·7	8·2
Greater than 100 ..	1·2	0	1·2	8·2	21·2	29·4

TABLE XI.

Comparison of Calculated and Observed Densities of Non-randomly distributed Species.

Species.	Locality.	Observed.	Calculated.	Obs. − Cal.
Eragrostis Barrelieri	S.F.	234·0	90·00	144·00
,, ,, ...	W.C.	1155·0	252·00	903·00
,, ,, ...	W.F.	1849·0	382·00	1457·00
Eragrostis Dielsii	S.C.	274·0	87·80	186·20
Enneapogon sp.	W.F.	118·0	90·75	27·25
Malva parviflora	S.C.	337·0	89·68	247·32
,, ,, ...	W.C.	224·0	69·23	154·77
,, ,, ...	W.F.	35·0	15·50	19·50
Schismus barbatus	W.C.	73·0	64·13	8·87
,, ,, ...	W.F.	279·0	46·43	232·57
Stipa variabilis	W.C.	131·0	96·75	34·25
,, ,, ...	W.F.	718·0	326·63	391·37
Tetragonia expansa	S.F.	131·0	29·20	101·80
,, ,, ...	W.C.	758·0	228·75	529·25
,, ,, ...	W.F.	335·0	114·75	220·25
Zygophyllum crenatum	S.C.	66·0	60·84	5·16
,, ,, ...	S.F.	107·0	76·08	30·92
Zygophyllum iodocarpum	S.F.	110·0	32·04	77·96
Zygophyllum ammophilum	S.C.	13·0	10·12	2·88
,, ,, ...	S.F.	44·0	11·70	32·30
Salsola Kali	S.C.	9·0	7·80	1·20
,, ,, ...	W.F.	97·0	32·10	64·90
Sida corrugata	S.C.	51·0	30·40	20·60
Sida intricata	S.F.	9·0	4·38	4·62
Lotus australis	W.C.	97·0	85·00	12·00
,, ,, ...	S.F.	22·0	12·80	9·20
,, ,, ...	S.C.	23·0	19·10	3·90
Centaurea melitensis	W.F.	316·0	178·50	137·50
,, ,, ...	W.C.	48·0	34·20	13·80
Argemone mexicana	W.C.	154·0	44·25	109·75
,, ,, ...	S.F.	12·0	8·82	3·18
,, ,, ...	S.C.	11·0	9·36	1·64
Danthonia sp.	W.F.	48·0	39·00	9·00
Convolvulus erubescens	S.F.	27·0	15·60	11·40
,, ,, ...	W.F.	44·0	23·57	20·43
Bassia lanicuspis	W.F.	23·0	18·00	5·00
Blennodia trisecta	S.F.	27·0	11·60	15·40
Lepidium papillosum	S.C.	10·0	7·80	2·20
,, ,, ...	S.F.	20·0	9·60	10·40
Erodium Botrys	S.F.	24·0	7·60	16·40
,, ,, ...	W.C.	5·0	5·70	−0·70
Echium plantagineum	S.C.	9·0	7·41	1·59
,, ,, ...	S.F.	8·0	6·40	1·60
Atriplex stipitatum	W.F.	12·0	4·55	7·45
Cassia eremophila	W.F.	10·0	8·50	1·50
Calotis cymbacantha	S.C.	13·0	8·58	4·42
Clianthus Dampieri	W.F.	7·0	3·99	3·01
Cucumis myriocarpus	S.C.	6·0	4·29	1·71
Citrullus vulgaris	S.C.	6·0	3·12	2·88
Sisymbrium officinale	S.C.	6·0	3·12	2·88
,, ,, ...	W.C.	5·0	3·99	1·01
Chenopodium carinatum	W.C.	5·0	3·00	2·00

Discussion and Conclusions.

At this stage we may revert to the questions asked on page 127.

(i). Has fencing increased the richness of the flora? From Table vi it appears that there is a greater variety of both annuals and perennials on the reserves than on the commons exposed to grazing; but reference to the statistical data in Table v indicates that these increases are at present in rare and not in common species. The striking differences in Plate ii are *not* accountable to an increase in floristic variety. Subsequent sampling may provide more reliable evidence on this point.

(ii). Has fencing increased the density of individual species? The change in density (Table v) is not commensurate with the obvious increase in plant cover shown in Plate ii. Despite the contrast between fenced and unfenced areas in the south, fencing has scarcely changed the number of perennials and it has actually halved the number of annuals. In the west, which was fenced earlier in the summer and which had been initially more heavily grazed, the perennials are increased nearly fourfold, although the annuals are only slightly changed. The decrease in annuals in the south reserve is probably due to the intense competition of such perennials as *Stipa* (cf. Pl. iii, figs. 1 and 4).

(iii). Is the change due to a profusion of annuals or to the spread of perennials? From the floristic list summarized in Table vi and from the data in Table v it appears that fencing has increased perennials relatively more than annuals, both in respect of species number and density of individuals. The effect of fencing upon annuals clearly depends upon the number and size of perennials present. If this conclusion is supported by subsequent sampling it will be important, for it will mean that fencing gives promise of a permanent improvement of the vegetative cover under these conditions.

(iv). Is more ground covered with vegetation, or is the vegetation merely taller? Some increase in mean area covered has occurred in the fenced areas but most of the visible differences between fenced and unfenced areas is due to the greater luxuriance of plants protected from grazing.

(v). Can one obtain some precise way of measuring the rate of colonization? In the 24 instances where individuals are randomly distributed it will be possible to measure accurately and quickly changes in density, due to season, grazing, competition, etc., by the random laying of sample strips and the determination of density from percentage absences (Table viii). Moreover, it is easy to obtain a variance for these determinations. The rate of colonization of non-random species can be followed with some precision by direct observations of density from sample strips laid repeatedly over the community, and from observations on the permanent quadrat.

(vi). Is the permanent quadrat an adequate sample of the community? The data assembled in Tables iii and iv show that the communities are homogeneous, and that the permanent quadrat, although it contains less than 40 per cent. of the total number of species, is large enough to manifest the homogeneity of the community.

(vii). What is the incidence of species with increasing area? The incidence of species follows the equation $n = 1{\cdot}87 \log a + b$, where b is the mean number of species per unit area, and n is the number of species on area a. It is, however, inadmissible to extrapolate far from the data, although, as is shown in Table iv, a fair estimate may be made of the number of species to be expected on areas as large as 8 acres.

It is instructive to compare the data reported in this paper with those from similar investigations in other regions. Steiger (1930) published values for the abundance of species in high and low prairie. His data have been analysed by Clapham (1936). The degree of non-randomness is judged by the value of the ratio of the variance in the Poisson distribution to the mean. In a perfect Poisson distribution this value is unity. If it exceeds unity there is aggregation among the plants. Clapham shows that most of the randomly distributed species occur in "low prairie" where the ground is open, while in "high prairie" where the grasses form a dense turf, most species are aggregated. Just as *Eragrostis Dielsii* at Broken Hill is randomly distributed in medium densities and aggregated at high densities (Table v) so in Nebraska *Eragrostis pectinacea* is almost random in low prairie and is aggregated in high prairie.

Protection from grazing for a short period has had a beneficial effect on the vegetation at Broken Hill. The study was made during a very good season, and the conclusions advanced above must be examined with this in mind. Before fencing can confidently be recommended to restore vegetative cover, four important questions must be answered:

(i). Will a response to fencing, similar to that in the Broken Hill area, be obtained on other plant communities, e.g. on mulga scrub, stony plains, sand hills, etc.?

(ii). Should the fencing exclude rabbits, or merely be stock-proof?

(iii). What rainfall is required to restore vegetation in a fenced area?

(iv.) Is fencing beneficial only when there is an assured supply of seed nearby?

All these questions must remain unanswered until more work is done, but it is instructive to compare the results of fencing at Broken Hill with those at Koonamore. In the reserve at Koonamore there was a fluctuating population of annuals and short-lived perennials. After twelve years, fencing had not restored the perennial flora. This contrast to the promising results at Broken Hill may be attributed to three handicaps at Koonamore: subnormal rainfall, grazing by rabbits, and the eroded condition of the land before fencing. At Koonamore the mean annual rainfall between the time of fencing and the last observations (1925–1935) has been only 70 per cent. of the mean (8·12″) for the last 27 years, whereas the mean at Broken Hill (9·31″) was exceeded in 1937 and 1939; also there has been a deficiency of effective rainfalls at Koonamore, while in the 33 months ending September 1939 there were at Broken Hill 18 months with rainfalls exceeding 0·3″. At Koonamore many species increased in numbers after the few effective rains, and of these a high percentage of those species unpalatable to rabbits (e.g. *Atriplex vesicarium* and *A. stipitatum*) survived the subsequent droughts. But the rabbit-proof fencing at Koonamore did not exclude rabbits, and they reached plague numbers in some seasons; under these conditions fencing which excluded stock was not effective in restoring the vegetation. Finally, the reserve at Koonamore was more heavily grazed before enclosure than the commons at Broken Hill, and erosion was so serious that in places the subsoil was exposed. The consequent destruction of seed bed and shortage of seed contribute doubtless to the contrasting results from the two areas; but the very contrast serves to emphasize that it would be premature to draw conclusions as to the effect of fencing either from Koonamore or from Broken Hill. Data from both these areas indicate that the pioneers on bare sand are annuals (in contrast to the perennials on sand dunes by the sea), and that perennials become established only after this preliminary colonization. At Broken Hill *Zygophyllum* spp., *Tetragonia*, and

Clianthus appear to be the best annual sand-binders. Of the perennials *Bassia* spp. are important as nurseries for other seed and *Sida intricata* and *Stipa* retain sand.

SUMMARY.

A comparative study has been made at Broken Hill of the vegetation of reserves protected from grazing and of the adjacent unfenced grazed commons.

The quantitative analysis includes observations on (i) the relation between species and area and (ii) the density and distribution of individual species in fenced and unfenced areas.

An analysis of species-area curves, obtained from sample strips of different sizes, showed that the communities studied were homogeneous, and that the species as a whole were randomly distributed.

The density and distribution of individual species was determined by sample strips 10m. × 0·15m., since most of the species recorded in these samples were found to have a frequency of 20 per cent. or less.

In 24 cases out of 75, it was found that there was no significant difference between the observed density and the density calculated from terms of the appropriate Poisson series.

In the cases of non-random distribution where the χ^2 test indicated that there was significant departure from Poisson distribution (random distribution), the calculated densities differed significantly from the observed densities.

It was found that the same species may be randomly distributed in one area and aggregated in another; normality of distribution disappears with increasing density.

The data indicate that protection from grazing during a period of less than two years has been (i) to increase markedly the growth of the individuals present before fencing. The increase in the height of *Stipa* is mainly responsible for the visible differences between fenced and unfenced sections in lightly grazed areas (south reserve); (ii) to increase the density of perennial individuals in heavily grazed areas (west reserve); (iii) to decrease the density of three of the most undesirable species, viz. *Malva*, *Lotus* and *Argemone*, which apparently cannot withstand competition; (iv) to reduce in good seasons the mean density of annuals by competition with robust perennials (south reserve); (v) to increase the variety of perennial and annual species.

Acknowledgements.

We have pleasure in expressing our thanks to the President and Council of the Linnean Society of New South Wales for a grant which defrayed travelling expenses and maintenance of one of us (I.M.P.) during the survey; to Miss Joyce Vickery of the National Herbarium, for assistance in collecting statistical data, in identifying species, and for information as to their palatability; and to Mrs. Morris of the Zinc Corporation at Broken Hill for her invaluable assistance in the field and her continued help in supplying information (notably supplementing the data in Table i).

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DESCRIPTION OF PLATES II-III.

Plate ii.

Fig. 1.—The south regeneration reserve and the adjoining common. Except for the track along the dividing fence, the common is well covered (left middle ground); *Stipa variabilis* dominant in the fenced area.

Fig. 2.—Western reserve and common. *Stipa variabilis* not so well developed as in figure 1; cattle grazing on common (right background).

Plate iii.

Fig. 1.—*Stipa variabilis* in south reserve, average height 0·75 metre.

Fig. 2.—Reserve No. 4. *Stipa variabilis, Salsola Kali* and ground cover of *Tetragonia expansa.*

Fig. 3.—*Stipa variabilis* and *Eragrostis Barrelieri* (centre) inside reserve (cf. fig. 4).

Fig. 4.—Prostrate and heavily grazed tufts of *Stipa variabilis* in west common. *Tetragonia expansa* in right background. Metre rule.

ON THE INTERPRETATION OF CERTAIN FEATURES OF AN EMBRYONIC SKULL OF PLATYPUS.

By H. Leighton Kesteven, D.Sc., M.D.

(Nine Text-figures.)

[Read 24th April, 1940.]

The present work was undertaken with the object of investigating further the development of the bone which de Beer and Fell (1936) identified as the alisphenoid. In collaboration with Furst, the author (1929) had described the basisphenoid as being developed from three centres of ossification, a central and two lateral. It appeared that it was these latter which de Beer and Fell had identified as the alisphenoid bones.

The study of the sections revealed several features of such interest that it was decided to model portion of the platypus head with a view to investigating these.

Material.—Besides the specimens which were used by the author and Furst in a previous study of the late embryonic skull (Kesteven and Furst, 1929), the head of an embryo measuring 140 mm. from tip of snout to end of tail along the dorsal surface was studied in sagittal and transverse sections. I have to thank Professor C. W. Stump for the opportunity to study this specimen and for its preparation. The head was cut off and then divided along the mid-sagittal plane into two halves. One half was cut in the sagittal plane, the other in the transverse vertical. A model was reconstructed from trans-sections numbers 227 to 327 inclusive. This model included, as well as the chondrocranium, portions of the parasphenoid (the mammalian pterygoid) and dentary bones, the second, fourth, fifth and seventh nerves, the internal cerebral and orbital branches of the carotid artery, portion of the large anterior ventral venous sinus with the commencement of its main efferent vein, and portion of the pituitary gland.

The model was made with a slight modification of the blotting paper wax method. Outlines were obtained by using a vertically arranged projecting lantern made for the purpose; they were coloured differentially for the various structures and cemented together with rubber solution. The adherence of the sections was all that could be required, but only after the surfaces had been coated with the solution twice, allowing the first coat to dry before applying the second.

The magnification of the model is twenty diameters. The portion included in the model measures 5 mm., one hundred sections, each 50μ thick. The model is 10·5 cm. long, that is to say, it is 0·5% over-long, a distortion so slight as to be negligible.

The sections will be returned to the Launcelot Harrison collection in the Anatomy Department at Sydney University, and the model will be lodged with them.

The embryo is No. T.O.4 in that collection, and the head has been catalogued as "Head of Platypus MM". The crown-rump measurement is approximately 56 mm., the snout-tail measurement approximately 140 mm.

I should like to thank Dr. A. A. Abbie for his assistance in the identification of the cranial nerves. My thanks are also offered Professor Burkitt as well as Professor Stump for the opportunity to use material from their departments at Sydney University. I have also to thank the Executive of the Directorate of The Goodyear Tyre & Rubber Co. (Australia) Ltd. for the equipment of my laboratory, wherein most of the work was done.

The Alisphenoid Problem.

In 1918 the author pointed out that there was strong evidence in favour of recognizing the "echidna-pterygoid" as the homologue of the tympanic wing of the mammalian alisphenoid. This was to a certain extent in agreement with a conclusion previously arrived at by Watson (1916), differing therefrom in that I was unable to agree that the mammalian alisphenoid was derived from the processus ascendens quadrati; de Beer and Fell were, therefore, in error in stating (1936, p. 21) that I had equated the echidna pterygoid with the processus ascendens.

Figs. 1, 2 and 3.—Transverse sections Nos. 261, 259 and 257 through the right half of the head of a Platypus embryo measuring 25 mm. from tip of snout to occiput.

De Beer and Fell (1936, p. 21) state that "a perichondral ossification is present in the ala temporalis, distinct from the alisphenoid. And since this alisphenoid is present *in addition to and distinct from* the '*Echidna*-pterygoid', the *Echidna*-pterygoid cannot be the alisphenoid."

I find that there is a definitely endochondral ossification of the processus alaris medially to the canal for the stapedial artery. This ossification takes the form of an almost continuous subchondral lamina, as indicated in Figures 1, 2 and 3, and spicular bone formation extending deeply into the cartilage. Posteriorly, medial to the exit of the artery (Fig. 1), the ossification does not reach the medial wall of the groove in which the artery lies, nor does it reach deeply to the medial wall of the canal itself (Fig. 2), but just in front of the canal it forms the medial wall of the groove (Fig. 3).

The relation to the vidian nerve is of particular interest. In this 140 mm. embryo the ossification lies lateral to and just clear of the nerve, but the vidian

canal is formed below the nerve by this ossification laterally and the pterygoid bone medially.

In this embryo there is no sign as yet of the medial area of ossification of the basisphenoid.

The next older embryo available for study is the 175 mm. specimen which was studied in 1929.

This is the specimen on which was based the statement that the basisphenoid ossifies from three centres; unfortunately the bald statement alone was made at that time. The lateral ossification in this skull has extended to enclose, almost completely, the arterial canal, and medially just on to the inferior surface of the horizontal portion of the basisphenoid cartilage. It will be noted that this extension is such that the whole of the vidian canal is now enclosed laterally by this ossification.

The prepared skull of this last specimen measures 25 mm. from the tip of snout to the occipital condyles. The next larger head measures 48 mm. In this the whole basisphenoid is completely ossified and there is no trace of any suture; on the contrary, there is complete fusion of the three centres of ossification. This last specimen was probably older than the 250 mm. embryo studied by Watson, in which also the three areas were completely fused, so much so, in fact, that there was no evidence of other than one continuous ossification.

When it is remembered that throughout the whole of the lower vertebrata the basisphenoid is ossified from two lateral centres of ossification, situated on either side of and, commonly, behind the pituitary fossa, the lateral areas in the basis cranii of the present embryos are at once recognizable as the two familiar areas of the saurians.

Almost without exception, in the mammalian skulls, one will observe that there remains a meniscus of cartilage between the developing alisphenoid and the lateral edge of the basisphenoid ossification. This meniscus is completely wanting; not only is this so, but those sharply-defined contiguous edges of ossification of the two bones in early stages of development are also completely missing in these embryos.

There is a still further difference observable. In most, if not all, mammals and marsupials the ala temporalis is rapidly ossified throughout its thickness, so that once ossification is fully under way one observes the basisphenoid and alisphenoid separated by the meniscus of cartilage at their contiguous edges. In the *Ornithorhynchus* embryos the median area of ossification develops on both surfaces of the cartilage, whilst the lateral areas extend on the ventral surface so as almost to meet the median area before the dorsal surface of the cartilage is ossified. From the appearances of the two younger embryos studied it would appear that fusion of the lateral and central areas takes place before the dorsal surface of the cartilage is ossified laterally.

From the foregoing evidence it is concluded that the basisphenoid bone in *Ornithorhynchus* is ossified from three centres, as previously stated, and that de Beer and Fell were in error when they thought to recognize the alisphenoid in the lateral area of ossification.

Before leaving this question it should be noted that the identification of the lateral area of the ossification as the alisphenoid, introduces the utmost confusion into the arguments relative to the homology of the mammalian pterygoid in the Monotremes.

This bone was identified as the lateral wing of the parasphenoid by Gaupp, and his conclusion has been accepted by most workers since his statement of the case appeared. It must, however, be remembered that the most weighty evidence on which the identification rested was that the bone closed the vidian canal ventrally. Now it has been very generally recognized that the vidian canal is that part of the parabasal canal which lies between the parasphenoid and the basisphenoid.

There is no doubt whatever that in *Ornithorhynchus* the vidian canal lies between the lateral ossification and the mammalian pterygoid; therefore, if this lateral ossification be the alisphenoid bone, then the vidian canal lies between the processus ascendens quadrati and the parasphenoid, that is, for all those who believe that the alisphenoid is derived from the ascending process.

This amounts to a *reductio ad absurdum*, for such a situation for a vidian canal is clearly an impossibility, if only because the parasphenoid could not come to underlie the processus ascendens.

This has not been cited as evidence against the identification of de Beer and Fell because the author (1) is unable to regard the alisphenoid as having been derived from the ascending process, and (2) has pointed out that in most primitive reptiles the vidian canal lies between the pterygoid bone and the parasphenoid; he therefore (3) concludes that the reptilian pterygoid and mammalian pterygoid are homologous, and (4) has also advanced reasons for believing that both these are derived from the parasphenoid bone.

The Relation of the Cranial Nerves and the Stapedial Artery to Certain Cranial Structures. Figs. 4, 5, 6.

The second nerve was traced from the chiasma forward through the peripituitary venous sinus and out of the cranial cavity through the pseudoptic foramen close to the floor. It then passes rostrad and laterad below the ophthalmic division of the fifth, and continuing in the same general direction, but with an inclination dorsad, reaches the eyeball.

The third nerve was exceedingly difficult to find and was not traced very far. It arises from the medial edge of the peduncle above, that is to say, anterior to, the interpeduncular ganglion and passes ventrad, laterad and rostrad in a fold of pia mater to reach the dorsal surface of the fifth nerve roots close to their junction with the ganglion. From here it was traced only a very short distance. It is confidently believed that it passes out of the cranial cavity in company with the first and second divisions of the fifth nerve behind and lateral to the processus clino-orbitalis. There is no doubt whatever that it does not emerge in front of the process through the pseudoptic foramen as stated heretofore.

The fourth nerve was traced from the lateral portion of the anterior medullary velum. It passes down close to the median surface of the backwardly-projecting posterior pole of the cerebral hemisphere and comes to lie upon the dorso-medial surface of the processus clino-orbitalis. The nerve continues forward and laterally, almost maintaining a constant level, so that, as the process inclines dorsad, the nerve passes below it and passes out between the process and the dorsal surface of the ophthalmic nerve. It crosses the nerve and then inclines ventrad so as to lie lateral to, and almost at the same level as, the optic nerve.

The very large roots of the fifth nerve are striking objects. It may be of interest to record that the motor division emerges at an appreciable distance from the sensory as a single root. The point of emergence is slightly anterior

to the motor root, and medially and dorsally thereto. This division of the nerve maintains its anatomical independence throughout its course; its branches do not commingle with those of the sensory division. The nerve may be very easily traced passing out laterally between the sensory roots and the floor of the cranium, then between the Gasserian ganglion and the roof of the cavum cochleare. Beneath the point of division of the mandibular ramus from the other two, the motor division turns sharply dorsad and rostrad and shortly thereafter it breaks up into its component nerves.

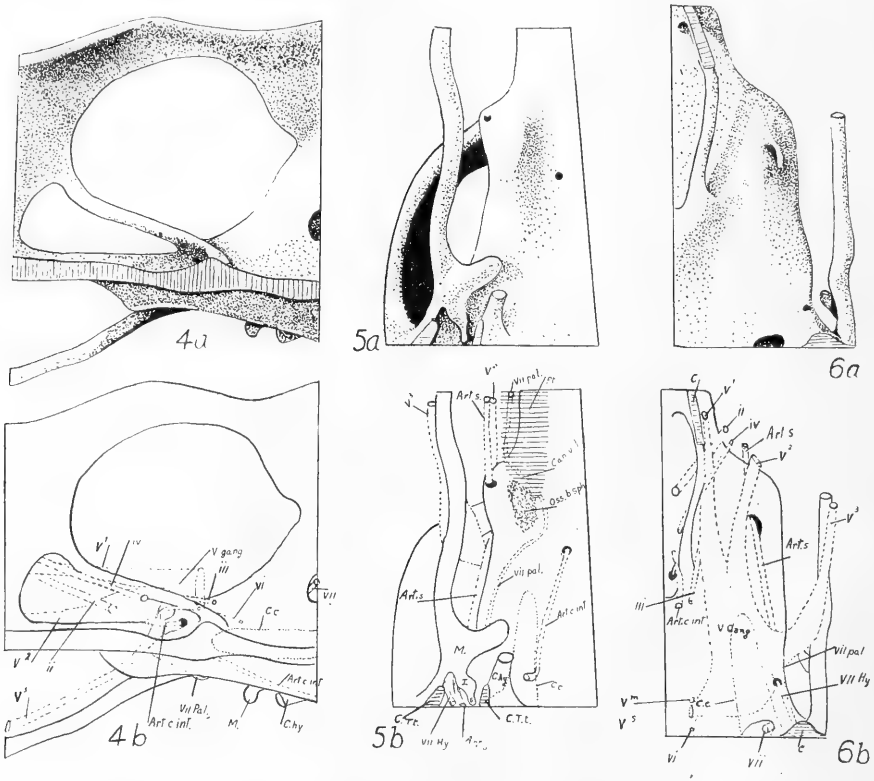

Fig. 4.—4*a*, Medial aspect of the model reconstructed from sections Nos. 227 to 327. 4*b*, Outline of same with the position of nerves and vessels indicated in dotted lines. (All the structures indicated, except nerves 3 and 6, are included in the model.)

Fig. 5.—5*a* and 5*b*, Ventral view and outline with nerves and vessels.

Fig. 6.—6*a* and 6*b*, Dorsal view of the cranial floor, with the roof removed, and outline showing the situation of the nerves and vessels.

The sixth nerve emerges from the ventral surface of the medulla medial to and in front of the roots of the seventh. The nerve passes ventrad and rostrad and then rostrad and laterad along the floor of the cranium. It is believed that it emerges from the cranium beneath the fifth nerve and courses forward ventral to the first branch, but it was lost almost as soon as it penetrated the membranous lining of the cranial cavity.

The seventh nerve passes almost directly into the anterior notch of the widely open internal auditory meatus, and then traverses the roof of the cavum

cochleare in a direction forward, laterally and slightly ventrally. The geniculate ganglion lies against the lateral wall of the cavum cochleare close to the exit of the nerve from the facial canal. From this point the palatine, vidian, nerve runs forward around the lateral edge and on to the ventral surface of the basis cranii. Below the basisphenoid region the nerve lies close to the medial edge of the lateral ossific centre of the basisphenoid bone, covered ventrally by the pterygoid. In my model the lateral portion of the pterygoid has been omitted in order to expose the nerve.

The ramus hyomandibularis runs caudad and very slightly laterad and passes below the malleo-otic commissure and above the incus and stapes, and then turns sharply ventrad behind the last two structures.

The stapedial artery lies below the hyomandibular nerve as they pass together medially to the tegmen tympani and between the incus and malleo-otic commissure.

The Processus Clino-orbitalis.

This has recently been identified by de Beer and Fell (1936) as the pila antotica. They remark: "It may be noted that the Monotremes are the only mammals in which the pila antotica is preserved, and it is therefore of additional interest to find that its morphological relations are similar to those found in the Reptiles. It is situated behind the oculomotor and trochlea nerves and the pituitary vein and in front of the trigeminal and abducent nerves." They further state that, in the Platypus, "the dorsum sellae" . . . "is directly continuous with the pila antotica on each side, just as it (or its homologue the crista sellaris) is in Lacerta".

The statement is inaccurate in more respects than one. Firstly, this pila is situated in front of the oculomotor nerve. Secondly, the suggestion that the abducent nerve lies behind the pila antotica is quite wrong, if it is intended to convey the idea that the nerve emerges from the cranium behind the pila. Thirdly, the pila antotica is not nearly so directly continuous with the crista sellaris as is the clino-orbital process with dorsum sellae.

Actually the relations of the structures to the process are, in the main, such as to contra-indicate the equation of de Beer and Fell.

In the saurians the pila metoptica lies between the optic and the oculomotor and trochlear nerves. It arises from the basis cranii just forward of and laterally to the hypophysis and passes dorsally and *forward* with little lateral inclination to become attached to the orbital cartilage.

In the saurians the pila antotica lies between the oculomotor and trochlear nerves in front and the trigeminal nerve behind. It arises from the extreme edge of the basis cranii a little distance lateral to and, commonly, a little in front of or a little behind the crista sellaris at the posterior boundary of the pituitary fossa. From this point the process extends dorsally and laterally with an inclination *caudad* either to join the taenia marginalis close to the antero-dorsal corner of the otocrane or that corner of the otocrane itself, or ends freely above.

If the processus be any of the saurian pilae retained in a modified form, then it appears more correct to equate it with the pila metoptica than with the antotic pila.

Actually it differs from the former far less than from the latter. It has in front of it one single nerve which lies behind it in saurians, otherwise its relation to the nerves is identical. Its direction is very emphatically that of the metoptic pila rather than that of the antotic and so also is its dorsal connection.

The relation to the pituitary vein is certainly against such an interpretation, but, even so, it is still possible to regard the process as a not very markedly modified metoptic pila.

When compared with the antotic pila, we find that this is in front of two nerves which should pass in front of the antotic pila at their point of emergence from the cranium; it arises from the lateral end of the dorsum sellae, that is, from the dorsal surface of the trabecular plate instead of from the edge of the trabecula or from the trabecular crest; and, finally, its direction is quite different and its dorsal attachment without parallel amongst the saurians. Briefly, at best it can only be regarded as a very profoundly modified pila antotica.

The Ossicula Auditus.

Lightoller (1939) has just advanced reasons for the belief that the malleus is the homologue of the quadrate and not of the articular. The conditions in the present embryo may be interpreted as giving strong support to that contention. They do not, however, appear to throw any further light on his suggestions as to the derivation of the incus, but rather raise an altogether new concept on the question.

When the model of the chondrocranium was made it became apparent that Meckel's cartilage was continuous with the chain of auditory ossicles and also with the otocrane. Further than this, it was at once apparent that the connection with the otocrane was by way of the malleus.

Now, here was a peculiarity. Reichert's theory recognized the malleus as the articular. If, then, this be the articular, how came it to be directly continuous with the cartilaginous skull. The articular is an ossification of the proximal end of Meckel's cartilage, and the quadrate stands between it and the skull.

If, as Lightoller suggests, the malleus be the quadrate, this connection becomes at once understandable, for throughout the whole of the amphibians the quadrate is in direct cartilaginous continuity with the skull.

With a view to investigating the question as thoroughly as a single specimen permitted, a larger model of the auditory ossicles was built. This is thirty times as large as the structures modelled. The structures were found in sections Nos. 298 to 326. The model should, therefore, have measured 4·35 cm. from front to back; actually it measures 4·5 cm.—a negligible distortion (Fig. 7).

Since it was unlikely that the articular had acquired a cartilaginous connection with the skull, this connection was deemed to be one of the quadrate attachments, and with this in mind the model was compared with the saurian quadrate. This comparison failed to yield any explanation of the attachment because the quadrate is not so attached to the cartilaginous cranium in any of the saurians.

Comparison with the amphibian quadrate, however, seemed to provide an explanation.

The model exhibits the following features: Without being appreciably thickened from side to side, the proximal end of Meckel's cartilage is quite suddenly widened in the dorso-ventral plane. The upper level of the cartilage is maintained nearly constant, but there is a slight inclination dorsad, and after a short interval the cartilage is continued backwards at what appears to be a resumption of the original shape. This, which has been designated the málleo-otic commissure, joins the otic capsule. The point of junction is opposite the internal auditory meatus; it is, therefore, situated close to the posterior end of the cavum cochleare and the anterior end of the cavum vestibulare where these lie one above

the other. The tegmen tympani springs from the outer wall of the otocrane immediately behind and below the point of attachment. The expanded portion of the cartilage is without doubt the malleus, and the manubrium stands down and inward, medially, from the body of the future bone. Immediately below the malleolar end of the commissure a stout process projects directly backwards from the body of the malleus. This, which is identified as the incus, maintains its thickness for only a short distance, then commences to taper and at the same point inclines mediad and terminates at the fenestra ovalis.

On the median surface of the body of the malleus just behind the point of junction with the commissure a thick boss projects medially. Seen from above, this appears as an abrupt thickening of the upper edge of the cartilage. From

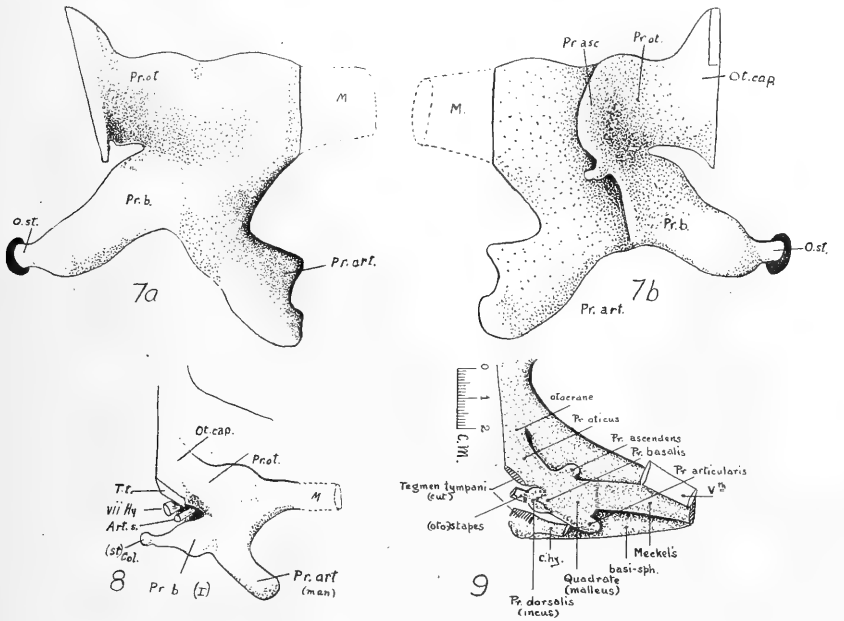

Fig. 7.—*7a*, Lateral, and *7b*, medial view of the model of the auditory cartilages reconstructed from sections Nos. 298 to 326.

Fig. 8.—The auditory cartilages attached to the otocrane, showing the situation of the hyomandibular nerve and the stapedial artery, between the processus oticus and the processus basalis.

Fig. 9.—Oblique view of model, showing the cartilages of the middle ear. The probable location of the future lines of division and the joints are schematically indicated. This drawing is by Dr. Lightoller.

below or in front, this boss is seen to be excavated anteriorly, and from the medial aspect it is found to lose in antero-posterior thickness, and in height from the body of the cartilage, from above downwards. In the middle of its dorso-ventral length there is a small, backwardly projecting spicule of cartilage on its free edge (Fig. 7*b*).

Before proceeding to the comparison with the amphibian condition it may be remarked that none of the recent saurians can be regarded as ancestral to the mammals, the Chelonians alone being sufficiently generalized to be regarded as

approaching the ancestral type. Therefore, if there be reason to believe that amphibian processes of the quadrate are recognizable in the malleus of the Platypus, their presence need not be regarded as a recurrence of the amphibian feature. On the contrary, they may be regarded as persistent features, carried down through the ancestral type, in which (e.g. the Cynodonts) the quadrate was even more amphibian in character than is that of the chelonians.

In the Amphibia the quadrate is attached to the skull by three processes, ascending, otic and basal.

The otic is attached to the otocrane well above the level of the basis cranii and in front of the basal process. The stapedial artery runs forward and the hyomandibular branch of the facial nerve backward between these two processes, close to the otocranial wall with the body of the quadrate lateral to them.

The resemblance of the malleo-otic commissure and the incudal process to these two processes of the amphibian quadrate is such as to suggest very strongly that they are homologous structures (Fig. 8).

The resemblance does not cease here. The amphibian quadrate carries, below the otic process, a larger or smaller remnant of the palatal process, and the ascending process is either attached to the quadrate directly just above the palatal process or rises from the palatal process close to the body of the cartilage.

The larger model shows that there is a short stout process on the antero-medial and superior edge of the malleus. This short process is certainly in just the position where the ascending process should be found if this be a quadrate, and moreover the spicule of cartilage attached to this vestigial "ascending process" may be interpreted as a more vestigial palatal process.

The resemblance goes even further than this. If one detach the stapedial component from the medial end of the incudal process and Meckel's cartilage from the distal end of the mass, there remains, attached to the skull by the otic process only, a quadrate, in which one may recognize not only all the three processes of attachment, but also the main articular ramus of the cartilage, this last being, of course, the manubrium.

It is, therefore, concluded that in *Ornithorhynchus* the malleus is derived from the quadrate, that the incus is derived from the processus basalis quadrati, and that the manubrium mallei is derived from the ramus articularis quadrati. It is believed that the stapes is the oto-stapes of lower vertebrata.

It is probable that the first reaction to this interpretation of the ossicula auditus will be that it is far too much to expect so simple an explanation, and modifications of the quadrate so slight as to permit of the recognition of all the features of the primitive amphibian bone. Actually, however, therein lies much of the strength of the suggestion.

Reichert's theory is faced with the same difficulties as the theory here advanced and with others as well. Under both assumptions it becomes necessary to explain the fusion of the whole chain of ossicles in this cartilaginous stage; for this fusion no explanation is apparent.

Reichert's theory is implicit with the belief that the articulo-quadrate joint was abruptly abandoned as the functional joint of the jaw, and was converted at once into the malleo-incudal joint. This appears to be a necessary assumption under this theory, for it is difficult to understand how otherwise the joint could have been preserved. Further, if the joint be the articulo-quadrate joint, then the body of the incus must be regarded as the ramus articularis quadrati, and it becomes necessary to postulate the addition of the manubrium mallei from

some other source. In the present instance there is added the difficulty of explaining the cartilaginous continuity of the malleus and the otocrane. It is difficult to understand how the portio articularis of Meckel's cartilage can have grown past the quadrate, which intervened, to reach the skull. Further, it becomes necessary to assume that the articulo-quadrate joint was obliterated by a cartilaginous continuum and was then re-established. A still further difficulty presents itself. The articular bone is altogether external and lateral to the membrana tympani, so that it becomes necessary to assume the destruction of the primitive membrane and its replacement by a newer one, or to assume that the articular has, in some way, come to penetrate the membrane without leaving any trace of the involution and closing of the perforation.

It is assumed here that the fusion of Meckel's cartilage and the quadrate took place between the body of the latter and the proximal end of the former, and that this took place after the temporo-dentary joint had commenced to function. It seems reasonable to believe that after the articulo-quadrate joint ceased to function, the portio articularis and its bone should become vestigial and disappear. The quadrate, however, was probably attached to the membrana tympani, as in most Chelonians. It is assumed that it retained this relation to the membrane as it became gradually reduced in size. The later development of a newer os tympani replacing the original functional attachment of the quadrate, the development of the joint between the root of the processus basalis and the newer relation to the oto-stapes are stages in the evolution which we have no information about. Since two of these three changes must be simply postulated under Reichert's theory, as under this, they are difficulties common to both.

Lightoller (1939) has suggested that the incus is derived from the dorsal process of the oto-stapes. He has kindly handed to me the accompanying drawing (Fig. 9), which schematically applies his suggestion to this stage of the platypus ear.

The suggestion is very tempting and offers a simple explanation of the joint between the future malleus and the incus. It is, however, not accepted unreservedly here because the model of the future ear ossicles suggests that the joint between the malleus and the incus will develop right across the cartilage in front of the boss which has been identified as the processus ascendens.

Even if that be so, it may still be the fact that the processus dorsalis of the oto-stapes has been incorporated, and that incorporation has conditioned the development of the joint at the point of fusion with the quadrate and its extension through the bases of the processes of the quadrate.*

I should like to thank Professor A. N. Burkitt and Dr. G. H. S. Lightoller for their advice and criticism of this work.

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* This interpretation of the origin of the ossicula auditus is not novel. Dr. Lightoller has drawn my attention to the fact that Huxley, in his Manual of the Anatomy of Vertebrated Animals (1871,, pp. 66 and 67), derived the malleus from the quadrate and the incus from the dorsal process of the otostapes. This, Lightoller remarks, is surprising for these views were not expressed by Huxley in his paper on the subject which appeared in 1869.

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Abbreviations used on the drawings.

Ali., Alisphenoid bone (Echidna-pterygoid); *Art.C.int.*, Internal cerebral artery; *Art.s.*, Stapedial Artery; *B.sph.* and *Oss.b.sph.*, Lateral area of ossification of the basi-sphenoid bone; *Can.vid.*, Vidian canal; *C.c.*, Cavum cochleare; *C.hy.*, Cerato-hyoid cartilage; *C.T.t.*, Tegmen tympani (cut away); *Dent.*, Dentary bone; *M.*, Meckel's cartilage; *Ot.cap.*, Otic capsule; *O.St.*, Oto-Stapes; *Pal.*, Palatine bone; *P.cl-o.*, Processus clino-orbitalis; *Pr.art.(Man.)*, Processus articularis quadrati (Manubrium); *Pr.asc.*, Processus palatinus, or perhaps processus ascendens quadrati; *Pr.b.(I.)*, Processus basalis quadrati (Incus); *Pr.ot.*, Processus oticus quadrati; *P.sph.*, Parasphenoid bone; *Pt.*, Pterygoid bone; *T.t.*, Tegmen tympani (cut away); vii *Hy.*, Hyomandibular branch of the viith nerve; vii *Pal.*, Palatine branch of the viith nerve.

STUDIES IN AUSTRALIAN EMBIOPTERA.

PART IV: SUPPLEMENTARY TAXONOMIC NOTES.

By Consett Davis, M.Sc., Lecturer in Biology, New England University College.
(8 Text-figures and 1 Map.)

[Read 27th March, 1940.]

Genus Metoligotoma Davis 1936.

Proc. Linn. Soc. N.S.W., lxi, 5–6, p. 248. Genotype, *Metoligotoma reducta* Davis 1936, l.c.—Re-defined, Davis, 1938, ibid., lxiii, 3–4, p. 227.

Metoligotoma rileyi, n. sp. Figs. 1–3.

♂. Length 17 mm.; head 3·5 mm. × 2·7 mm. General colour (dry) dark chocolate-brown. Head (Fig. 1) with small eyes, sides of head behind eyes slightly sinuous, converging posteriorly. Antennae incomplete. Mandibles as in other species of *Metoligotoma*. Wingless. First segment of hind tarsi with a terminal ventral bladder; medial ventral bladder not apparent. If this bladder is uniformly absent, the species is exceptional in the genus; it is unsafe to generalize on a single dried specimen. Terminalia (Figs. 2–3) agreeing in general structure with other members of the genus; posterior process of right hemitergite ($10RP_1$) curved outward, slightly dilated terminally; dorsal process ($10RP_2$) with free edge evenly rounded, process directed upward in the type. Left hemitergite (10L) small; process (10LP) long, rather broad, expanded terminally, obliquely truncate, the oblique face directed backward and to the left, somewhat roughened. Left cercus (LC) one-segmented (i.e. the two larval segments fused); composite structure slender, incurved, obtuse terminally; cross-section approximately uniform throughout. Inner margin of LC smooth except for traces of a few subterminal nodules. Hypandrium (H) and its process (HP) normal for the genus; left cercus-basipodite (LCB) obtuse, irregularly tapered, sclerotized only terminally and subterminally on outer side. Setae of left cercus long and numerous.

♀ unknown.

Locality.—Townsville, Q., –/8/1903, F. P. Dodd. Holotype ♂ in the British Museum of Natural History. Named after Mr. N. Riley, Keeper, Entomology Department, British Museum.

This record extends the range of *Metoligotoma* a considerable distance to the north, and forms an interesting link with *Burmitembia venosa* Cockerell 1919 (Burmese Amber, ? Miocene), of which the genus *Metoligotoma* may be a direct descendant. The terminalia of *M. rileyi* agree more closely with *B. venosa* than do any of the more southern species of *Metoligotoma*.

The species may be fitted into the key to the genus (Davis, 1938, p. 250) at the commencement (before *M. anomala*), being separable from all other known species on the form of the left cercus and process of the left hemitergite.

METOLIGOTOMA REDUCTA Davis 1936.

This species (re-defined, Davis, 1938; figs. 1–4) has been recorded (l.c.) from the Central Coast of New South Wales (Otford to Broken Bay, and inland). In this region, it is specifically distinct from *M. illawarrae*; at the previous most northerly record (north of Broken Bay) it occurs in the field beside *M. illawarrae illawarrae*, without any trace of intergradation.

Map 1.—Distribution of subspecies of *Oligotoma gurneyi* Frogg.: *O. gurneyi gurneyi*, 1-1 (to south and east); *O. gurneyi centralis*, 2-2 (to south); *O. gurneyi spinulosa*, 3-3 (to west); *O. gurneyi subclavata*, 4-4 (to north).

Each dot represents a record. Dots enclosed in more than one range represent intermediates between respective subspecies.

It is uncertain on the present data whether the range of *O. gurneyi subclavata* should be closed at the Gulf of Carpentaria, or carried further east to include the record from Chinchilla, Q., as an intermediate between it and *O. gurneyi gurneyi*. Further collecting in North-East Australia should decide this point. The two alternative ranges are shown as dotted lines, each extending to '4?'.

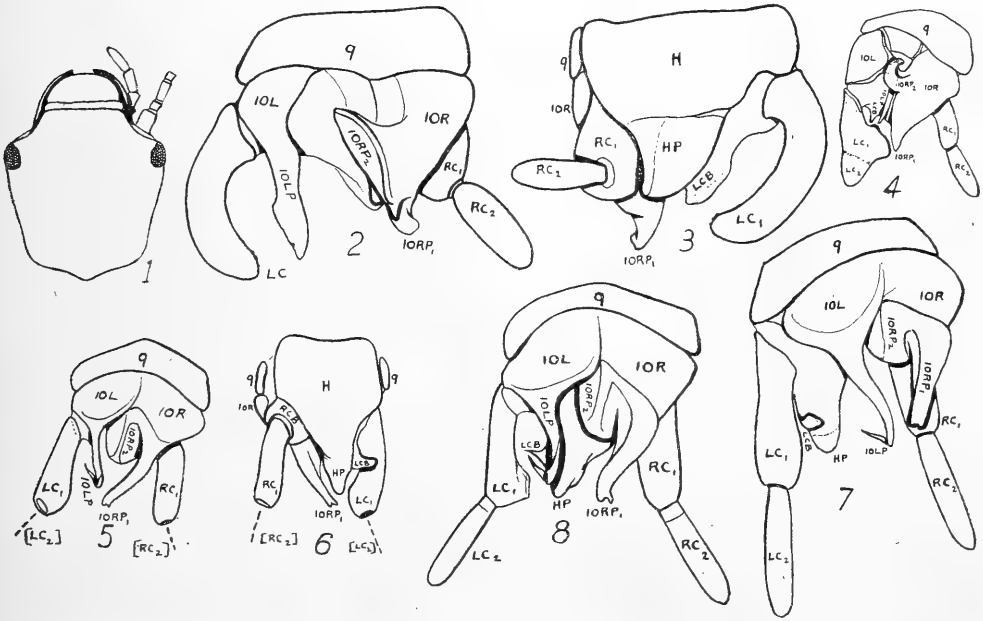
Recent records of males from the North Coast of New South Wales (Crescent Head, nr. Kempsey, 13/8/39; Mingaletta, nr. Kempsey, 15/8/39; Port Macquarie, 15/8/39) suggest that a northern race of *M. reducta* occupies this region. These series agree in size and colour with *M. reducta*, the terminalia agreeing in the general structure of the hemitergites and hypandrium, and their processes. However, both the left cercus and the left cercus-basipodite suggest an approach to *M. illawarrae*, the former in having the distal part of the inner face much less smooth in outline than in *M. reducta*, the latter being more acute, although not truly spinescent as in *M. illawarrae*. The three series differ slightly among themselves, as do the individuals of the longest series (Crescent Head) *inter se*, suggesting an unstable population.

It seems desirable to refrain from naming this northern race until more locality records, especially intermediate ones, are available. The facts suggest an unusual form of 'Rassenkreis', a common population (North Coast of New South Wales) possibly diverging gradually so as to appear as two distinct species in the south (Broken Bay and southwards). Normally, a 'Rassenkreis' comprises a circle of races, the species having spread in two directions, and, later, the extreme ranges having come into contact by closing of the circle; at this point of meeting,

isolation has rendered the populations specifically distinct in their behaviour, though they are linked, around the full circle, by a free-breeding chain of populations. Here, however, the two lines of migration (from the North Coast southwards) would seem to be coincident, culminating in populations just as distinct. Investigation of the populations north of Broken Bay (e.g. near Newcastle) should give interesting results.

Males from Crescent Head, Mingaletta, and Port Macquarie have been deposited in the Macleay Museum.

A series of males from Leichhardt, Sydney (coll. F. Hasemer) seems to agree with these North Coast forms; this population was probably introduced to Leichhardt with a stag's-horn fern (*Platycerium*), in and near which the specimens were collected at Leichhardt. The exact origin of this series is therefore doubtful.



Figs. 1-3.—*Metoligotoma rileyi*, n. sp., holotype ♂. 1. Head from above, × 8. 2. Terminalia from above, × 20. 3. Terminalia from below, × 20.

Fig. 4.—*Notoligotoma hardyi* (Fried.), ♂ from Midland, W.A. Terminalia from above, × 20.

Figs. 5-6.—*Oligotoma gurneyi* Frogg., ♂ from Lalla Rookh, N. W. Australia. (Intermediate between subspecies *subclavata* Davis and *spinulosa* Davis.) 5. Terminalia from above, × 20. 6. Terminalia from below, × 20, left cercus-basipodite bent outwards.

Fig. 7.—*Oligotoma gurneyi* Frogg., ♂ from Hermannsburg, Central Australia, with similar characters to ♂ from N. W. Australia. Terminalia from above, × 20, somewhat distorted.

Fig. 8.—*Oligotoma gurneyi spinulosa* Davis, ♂ from Geraldton, W.A. Terminalia from above, × 30.

All setae omitted; all figures based on camera-lucida outlines.

9, ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, $10RP_2$, outer (or posterior) and inner processes of 10R; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LC, one-segmented left cercus; LCB, left cercus-basipodite; H, hypandrium; HP, process of H.

Genus Notoligotoma Davis 1936.

Proc. Linn. Soc. N.S.W., lxi, 5–6, p. 244. Genotype, *Oligotoma hardyi* Friederichs 1914, *Rec. W. Aust. Mus.*, vol. 1, pt. 3, p. 241.

Notoligotoma nitens Davis 1936.

Proc. Linn. Soc. N.S.W., 1936, lxi, 5–6, p. 246, figs. 9, 16, 23, 30, 37, 39–41.

In the Museum of Comparative Zoology, Harvard University, is a series of females and immature specimens labelled : 'Oligotoma gurneyi Frogg.; Sydney, N.S.W., T. Steel, iii.05.' They are certainly from the series noted by Froggatt (1905) as occurring in great numbers at Pyrmont (Colonial Sugar Refining Co.'s building; Mr. Steel, then an officer of that company, collected Froggatt's material). This series was referred by Froggatt (l.c.) to *O. gurneyi*, and by Friederichs (1923, p. 1) to *O. agilis* Frogg. (a synonym of *O. gurneyi gurneyi*; v. Davis, 1938, p. 252 et seq.); this course was allowed (Davis, 1938, p. 254), though previously (1936, p. 237), the different—and correct—course was suggested.

The specimens prove to belong to a genus other than *Oligotoma*, having two well-developed hind metatarsal bladders. On this character, they would be referable to *Notoligotoma nitens* or to one of the Sydney species of *Metoligotoma* (*M. reducta*, *M. illawarrae*). The reference to *N. nitens* seems reasonably certain, as the females agree in the colour and form of thoracic nota. Three penultimate instar males were preserved; although none have wing-buds (which would prove immediately that they belonged, not to *Metoligotoma*, but to *Notoligotoma*), the terminalia, with their incipient changes, are characteristic of this stage of *Notoligotoma*.

The record seems to represent a case of an indigenous species reaching great abundance under artificial conditions set up by man (high humidity and temperature from steam-outlets; abundant food in the form of raw sugar).

Notoligotoma hardyi (Fried.). Fig. 4.

The following records of mature males of this species represent new localities: Midland, near Perth, W.A., vi.1936 and vii.1938 (Western Australian Museum); Rockhampton, Q., vii.1937, viii.1937 and vi.1938, coll. W. J. S. Sloan.

The terminalia of a specimen from Midland, W.A., very close to the type locality, are here figured (Fig. 4); the earlier figure (Davis, 1936, fig. 8) is unsatisfactory, as it omits the sclerite basally separating the hemitergites of the tenth abdominal segment.

Genus Oligotoma Westwood 1837.

Trans. Linn. Soc. London, xvii, p. 373. Genotype, *Oligotoma saundersii* Westwood 1837, l.c.

Oligotoma gurneyi Froggatt 1904.

Proc. Linn. Soc. N.S.W., xxix, p. 672.

The following intermediates between subspecies have already been recorded:

O. gurneyi gurneyi Frogg.–*O. gurneyi centralis* Davis 1936 (Proc. Linn. Soc. N.S.W., lxi, 5–6, p. 237): Left cercus-basipodite of *centralis*, remainder as in *gurneyi*: Lucindale; Adelaide (S.A.); Lady Julia Percy Isd., Vic. (forma aptera) (Davis, 1936, p. 239; 1938, p. 254).—Outer process of right hemitergite of *centralis* or *subclavata* Davis 1936, remainder as in *gurneyi*: Chinchilla, Q. (Davis, 1938, p. 254).

The following additional intermediates are recorded:

(1). ♂ from Forest Reefs, N.S.W. (Museum of Comparative Zoology), almost typical of *O. gurneyi gurneyi* (the nearest known locality of which is Nyngan, N.S.W.), but with the termination of the outer process of the right hemitergite showing a slight tendency to the bidentate form seen in the Chinchilla specimens.

(2). ♂ from Lalla Rookh Station, North-West Australia (Western Australian Museum; Figs. 5–6), is suggestive of *O. gurneyi spinulosa* Davis 1936, the subspecies occupying the more southerly parts of Western Australia (infra); it differs markedly in the left cercus and cercus-basipodite. The first segment of the left cercus (LC_1) is only very slightly clavate, as in the North Australian *O. gurneyi subclavata*; the present specimen has this segment less clavate even than in *O. gurneyi subclavata*, whereas in *O. gurneyi spinulosa* it is produced inward subterminally more markedly than in any other subspecies. The left cercus basipodite (LCB) is blunt, in contrast to the spinescent structure of *O. gurneyi spinulosa*; it agrees with *O. gurneyi subclavata*, or perhaps more closely with *O. gurneyi centralis*.

This specimen may represent a distinct subspecies, but it may temporarily be regarded as an intermediate; the difference is merely a matter of degree. In size it agrees rather with *O. gurneyi centralis* and *O. gurneyi spinulosa* than with *O. gurneyi subclavata* (length, in alcohol, 11 mm.; head 1·9 mm. × 1·4 mm.; forewing 8 mm. × 2·2 mm.; hindwing 7 mm. × 2·2 mm.). The general colour (pale reddish-brown) is paler than in *O. gurneyi spinulosa*, but the specimen is apparently incompletely melanized and sclerotized after ecdysis.

(3). ♂ from Hermannsburg, Central Australia (coll. H. J. Hillier; British Museum of Natural History): Agrees almost exactly with (2); the terminalia (Fig. 7) had been somewhat distorted on a slide mount, which probably explains the less clavate appearance of the first segment of the left cercus. The dimensions are: length 10 mm.; length of head 1·5 mm.; length of forewing 8 mm. The left cercus-basipodite is closer to *O. gurneyi centralis* than in the Lalla Rookh specimen.

Hermannsburg represents a focal point to the ranges of *O. gurneyi centralis*, *O. gurneyi subclavata* and *O. gurneyi spinulosa*; this supports the present classification of (2) and (3), and the consideration of these three units as subspecies.

(4). ♂ from Geraldton, W.A. (British Museum): This is an almost typical example of *O. gurneyi spinulosa*, extending the range of this subspecies from the Lake Violet-Morgan's region to the West Coast. The terminalia (Fig. 8) show only the slightest differences (in the left cercus and outer process of the right hemitergite) from typical examples (Davis, 1936, fig. 3). The dimensions are: length (relaxed) 11 mm.; head 1·8 mm. × 1·4 mm.; forewing 7 mm. × 1·6 mm.; hindwing 6 mm. × 1·7 mm. The colour agrees with the type series.

Note.—The further records have tended to confirm the subspecific (racial) status, as against specific, for *Oligotoma gurneyi* (*gurneyi, centralis, spinulosa* and *subclavata*). The distribution of the four races is indicated in Map 1. Each dot represents a record; the dots enclosed in two or more distribution-lines represent intermediates. The greatest hiatus for records occurs in North-East Australia; the range of *O. gurneyi subclavata* has been provisionally sketched to include this area, so as to make the Chinchilla, Q., record an intermediate between *gurneyi* and *subclavata*. On the present data, this record might just as well represent *gurneyi* × *centralis*. Actually, it is predicted that an undiscovered subspecies, tending towards *O. albertisi* Nav., may occupy North-East Australia; this New Guinea species has the outer process of the right hemitergite and the

left cercus-basipodite in agreement with the Chinchilla specimens, and the left cercus as in *O. gurneyi subclavata*, but it differs from them and all subspecies of *O. gurneyi* in the lack of the terminal hook on the process of the left hemitergite.

The differences between the subspecies of *O. gurneyi* are far more striking than many of the so-called specific differences between the Asiatic 'species'. In view of the above data, it seems likely that many of the Asiatic 'species' have been classed in too high a category.

OLIGOTOMA SAUNDERSII Westwood 1837.

Syn. *O. latreillii* (Ramb.); v. Davis, 1939.

New Australian records for this species, based on mature males, are as follows: Mt. Larcom, Q., x.35 and 10.viii.36; Thangool, Q., 11.ii.36, coll. W. J. S. Sloan.

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CORRIGENDUM.

Davis, 1938 (Part iii of this series): Page 271, line 7, *for* levator *read* flexor

NOTES ON THE LIFE-HISTORY OF *LIMNOPHORA NIGRIORBITALIS* MALL. (DIPTERA, ANTHOMYIIDAE.)

By Kathleen M. I. English, B.Sc.

(Seven Text-figures.)

[Read 27th March, 1940.]

This fly was identified for me by Mr. J. R. Malloch, who described the female in 1924. The type, a single female, was collected by the late Dr. E. W. Ferguson in 1923, and it is now at the School of Public Health and Tropical Medicine in Sydney, where Mr. F. H. Taylor allowed me to examine it.

A description of the male, not previously recorded, is given below, together with a more detailed description of the female than that given by Malloch.

Description of the Adult.

♂, ♀. Frons about one-third of head-width, sides almost parallel, in profile sloping straight back, making with the face an angle greater than a right angle. Fronto-orbital bristles: anterior pair on each side well developed and curved inward, almost meeting in the centre line; posterior pair on each side smaller and curved slightly outward and backward. Two pairs of well-developed vertical bristles. Antennae with lower apical angle rounded, upper one squared; arista pubescent, but not densely so, about equally haired above and below. Face silvery, concave, without carina, and devoid of bristles between the bases of antennae and vibrissae. Proboscis thick, with fleshy labellae; palpi clubbed slightly. Mesonotum brown with three darker brown stripes not distinctly marked; pleura and margins of mesonotum lavender-grey; some brown markings on upper part of pleura; scutellum brown. Dorsocentrals 2 + 3. Pteropleura bare, hypopleura bare. Sternopleurals 3, not forming an equilateral triangle, and unequally developed, the postero-dorsal one very long and strong. Prosternum with fine setulae on side margins; basal abdominal sternite with fine hairs. Fore tarsus widened, fore tibia without median bristle. Wings clear, third wing-vein with minute setulae at base on upper and lower surfaces. Calyptrae white; halteres yellow. Length 3½ to 4 mm.

♂. Frons velvety-black except for a narrow central triangle, with base at ocelli and apex towards antennae, which is dull black. Cheeks do not project in front of eyes, so are not normally visible in profile. Abdomen: dorsal surface (Text-fig. 1), first tergite dark brown with a small spot of grey showing on the outer edge on each side; second and third tergites with a central fore and aft strip of dark brown and a velvety-black patch on each side of it, leaving a triangular piece of silvery-grey on the anterior margin of each side, the apex of the grey triangle pointing inward; fourth tergite with a central triangular patch of dark brown, grey on each side. Ventral surface lavender-grey. Legs black, except the fore tarsi and apical segment of middle and hind tarsi, which are

yellow with black bristles; and the ventral surfaces of the femora, which are greyish. Apical spurs on fore and middle tibia well developed, smaller on hind tibia; one weak median dorsal bristle on hind tibia.

♀. Frons, viewed from above, velvety-black on sides, dull black in centre; viewed from front or side the centre part is dark bronze. Cheeks project in front of eyes, so they are visible in profile. The dorsal surface of the abdomen is brown, with grey markings as in the male, except that the grey triangles on the second and third segments are much smaller and may hardly show at all; the ventral surface is lavender-grey with brown on the outer edges of the first three segments. Legs: tarsi black, tibiae dark brown; dorsal surface of femora brown, ventral surface greyish. Apical spurs well developed on middle tibia, weaker on fore and hind tibiae; one median postero-dorsal bristle on middle tibia, and one median dorsal bristle on hind tibia.

No adults have been taken when net collecting.

Classification.

In Malloch's key to the Sub-families of the Australian Muscidae (1925), the fly runs down to the Phaoniinae, except that it does not agree exactly with couplet three, for the two upper pairs of orbital bristles are directed slightly outward. In his key to the Phaoniinae (1925), the fly runs down to the genus *Limnophora*; and in his key to the species (1925*a*), it runs down to *nigriorbitalis*, except that couplet four, which reads "Entire frons including orbits opaque deep black", would be more accurate with the addition of the words "when viewed from above", as when viewed from the front or side the centre appears bronze in the female.

In Curran's key to the Muscidae (1934) the fly runs down to the couplet containing *Limnophora* and *Pseudolimnophora*; it passes the former and goes on to the genus *Pseudolimnophora*.

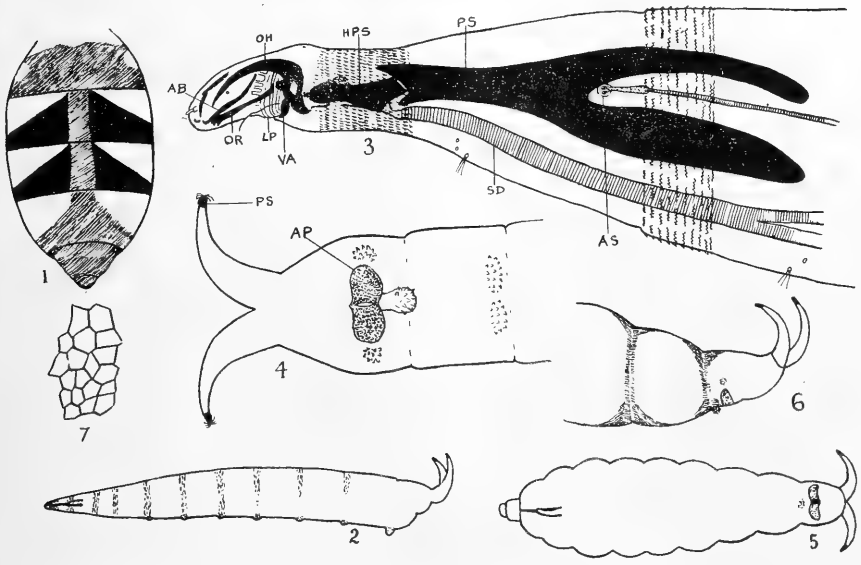
In Collin's key to the British Limnophora (1921) it runs down to the sub-genus *Pseudolimnophora*, with one exception: the frons in profile is straight and sloping; the keys says, "Frons in profile convex and sloping".

The Larva (Text-figs. 2, 3, 4).

When alive the larva is creamy-white; the skin is transparent; the internal organs can be seen, and the tracheal tubes can be traced from the anterior to the posterior spiracles; the jaws can be seen even if retracted. When killed, the skin becomes opaque. The shape is cylindrical, it tapers gradually in front to the very small head; the posterior segment narrows rather abruptly, then divides into two divergent horns with black tips. Larvae grow to 8 mm. in length, and to 1 mm. in width.

There are three thoracic and eight abdominal segments. The anterior portion of the first thoracic segment (Text-fig. 3) is covered with rows of tiny hooks with points directed backward; this portion is drawn inward when the head is retracted; the posterior portion of this segment bears the anterior spiracles. The second and third segments each have, on their anterior border, about ten rows of backwardly-directed hooks; the hooks do not form continuous rows, but are arranged in little groups. The ventral surface of the first segment bears at least two pairs of sensory organs, each in the form of a circular disc; the second and third segments each have at least one pair of similar organs. Each of the three segments bears also another pair of sensory organs on the ventral surface, in the form of a tuft of three hairs. Similar organs are described by Keilin (1917) for *Melanochelia riparia* Rond.

On the anterior borders of the first seven segments of the abdomen are broken rows of small backwardly-directed hooks; there are approximately eight rows on the first segment, and they are reduced gradually to five rows on the dorsal part of the seventh. The rows of hooks extend all round on the first three segments, but are more and more restricted to the dorsal surface on succeeding segments (Text-fig. 2). On the anterior border of the ventral surface of segments two to seven there is a pair of papillae bearing larger hooks; the first papillae



Text-figs. 1-7.—1. Abdomen of male, dorsal surface, × 24 (approx.).—2. Larva, side view, × 7.—3. Anterior end of larva, × 100; *ab*, anterior band; *as*, anterior spiracle; *hps*, hypopharyngeal sclerite; *lp*, labial palp; *oh*, oral hook; *or*, oral rod; *ps*, pharyngeal sclerite; *sd*, salivary duct; *va*, ventral arch.—4. Posterior end of larva, × 20; *ap*, anal plate; *ps*, posterior spiracle.—5. Pupa, ventral surface, × 8 (approx.). —6. Posterior end of pupa, side view, × 14 (approx.).—7. Network pattern on surface of pupa, × 48.

are very small, succeeding pairs are larger. These pads are used in locomotion. On the ventral surface of the eighth segment (Text-fig. 4), at the anterior edge, is a rounded flexible process bearing hooks; behind this is the anal plate, on each side of which is a small prominence bearing hooks. Posteriorly the segment divides into two horns, the tips of which are chitinized and bear the spiracles.

The head (Text-fig. 3) is very small and can be completely retracted. It bears paired antennae, maxillary palps, sensory organs and large labial palps.

The buccopharyngeal armature consists of three main parts, heavily chitinized. The posterior portion is the basal piece or pharyngeal sclerite, consisting of an anterior, elongated, central portion, and posteriorly of paired dorsal and ventral prolongations or horns; the dorsal horns are separate, but the ventral ones, though lying as far apart as the dorsal pair, are connected by thin chitin, extending from their ventral edges and joining in the median line. Anteriorly, this piece articulates with the hypopharyngeal sclerite, which consists of elongated side-pieces, connected by thin chitin for part of their length; below it are slender

rods, and from the posterior end the large salivary duct is given off. Anteriorly this piece articulates with the posterior prolongations of the paired oral hooks. The oral hooks are long and narrow; they are joined by the median ventral arch. Connected also with the hooks, and moving in conjunction with them, are the oral rods and anterior bands.

The larvae are carnivorous; they kill small worms and larvae; when kept in tubes together they do not readily kill one another, but will do so eventually. The large size of the salivary duct, the large labial palps, and the presence of the median ventral arch are all, according to de Vos-de Wilde (1935), characteristic features of carnivorous larvae.

The larvae are amphineustic when full grown. Very young larvae have not been found, so it has not been ascertained if they are amphineustic in all stages; but immature larvae have been examined, in which the posterior spiracles and the buccopharyngeal armature were not fully chitinized, but anterior spiracles were present.

The Pupa (Text-figs. 5, 6, 7).

The pupa is cylindrical in shape; it narrows abruptly anteriorly to a beak-like projection formed by the first and second thoracic segments, and it tapers gradually to the last segment, which divides into two horns, as in the larva. Pupae vary in length from 4 mm. to 6 mm., and in breadth from 1 mm. to 1·5 mm. They are brown in colour, and the surface is marked with a network pattern (Text-fig. 7) of dark brown lines on a lighter brown background. On each side of the beak, and extending on to the next segment, is a raised fold; this is the line on which the pupa splits for the emergence of the fly. On the ventral surface of the second to the seventh abdominal segments there are hooks among the network lines; these are the hooks of the larval papillae. On the eighth segment the central process persists as a small prominence bearing hooks. Behind this is the anal plate, red-brown in colour, not covered by the surface network, and with a dark-brown centre. On each side of the anal plate are hooks in the network.

Clean wet pupae are transparent; the larval jaws can be seen; and, as development proceeds, the shape of the imago can be seen, the dark legs becoming more and more distinct. The imago lies in the anterior portion of the pupa, leaving the two posterior segments empty. Pupae found in earthy moss are sometimes very dark and dirty, and are not then transparent.

Occurrence.

Larvae and pupae have been collected in various streams in the Yass district between September and May, over several years. They are to be found in moss or water-weeds, in running water, or at the edges of streams. In some instances they were in moss some inches above water; and once they were several inches below water; the river had risen and the water had been well over the moss for ten days.

They may be found in well-grown cushions of moss by parting the leafy growth; they are not seen on top of the moss. But the most satisfactory method is to collect the moss, wash it in a strainer with a fairly fine mesh, and then examine. This method is very necessary when the moss is stunted, as the larvae are then amongst the roots. When climatic conditions had caused the moss to die off, or become very scarce, larvae were found in water-weeds and the matted root-growth of willows.

They are found singly, and are most numerous in well-grown moss cushions, where one might find half a dozen in a few moments; but usually about 8 or 10 larvae and pupae in an hour's search would be a good catch.

Larvae have been found in each month from September to May; except January, when no collecting was done, and March, when very little was done. Pupae were found in each month from September to May, except January. Adults emerged in each month from October to May, except March.

More than fifty larvae were collected, mostly full grown or nearly so. Only three immature larvae were found; they were 3 mm. and 3·5 mm. in length, and were found in October, the month in which most collecting was done.

The larvae were kept in corked tubes with wet moss, but no serious effort was made to give them suitable conditions, and usually they pupated soon after capture, or died. In one case two larvae, collected in May, were put into a tube; one pupated in August, having eaten the other in the interval.

The length of the pupal period was not determined accurately, as most adults emerged from collected pupae; or when larvae pupated in captivity the actual date of pupation was not obtained. The most accurate records obtained showed pupal periods of about two weeks in February, and about three weeks in October and May.

Summing up, from the records obtained, it may be said that larvae can be found all the year round, pupae from August to May, and adults from September to May.

More than thirty adults were obtained; there were nearly twice as many males as females. They lived only a day or two, but that may have been due to unsuitable conditions.

The flies emerged in the mornings, usually before ten o'clock. Emergence can take place even if the pupa is dry; one fly emerged from a pupa which had been dry for nine days. Often the anterior cap does not break off when the fly emerges and the parts come together again, so it is not always obvious whether a pupa is empty or not.

Larvae and pupae are similar in many respects to the same stages of *Melanochelia riparia* Rond., described briefly by Halliday (1857), and in detail by Keilin (1917), which are found under the same conditions in Europe.

Johannsen (1935) gives a key to the larvae and puparia of the aquatic Anthomyiidae of North America, in which this species runs down to the genus *Limnophora*. His three described species are found under conditions similar to those in which this one occurs.

Acknowledgements.

The writer wishes to thank Mr. J. R. Malloch and Mr. F. H. Taylor for their help; and the late Mr. A. L. Tonnoir and Dr. I. Mackerras for the loan of literature.

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A PERMIAN BLASTOID FROM BELFORD, NEW SOUTH WALES.

By Joan M. Crockford and Ida A. Brown, Department of Geology, University of Sydney.

(Plate iv; one Text-figure.)

[Read 24th April, 1940.]

During a recent visit to the Hunter River district the writers collected two specimens of radial plates of a Blastoid. Since no Blastoid has been described so far from the Permian of New South Wales, it seems advisable to place on record the occurrence of this fossil. Probably further collecting will reveal other and better specimens.

One specimen, (A) (39158, Australian Museum Collection), comes from the hillslope about 100 yards west of Jump-Up Creek, in Portion 14, Parish of Belford, 2½ miles north of Belford Railway Station; the other, (B) (39159, Aust. Mus. Colln.), comes from Jump-Up Creek, below the Railway Bridge, half a mile west of Belford. They are both from the same horizon, the Fenestella Shale Bed, in the Upper Marine (Permian) Series.

Tricoelocrinus (?) belfordi, n. sp.

The specimens are external moulds in sandy shales containing abundant Fenestrellinidae and crinoid stems. Each specimen consists essentially of a single large radial or forked plate, with portion of the ambulacral plates.

In specimen A the radial plate is 3·5 cm. in length, and 1·7 cm. in width, the ratio limb to body being 15 to 20. The inter-radial sutures are comparatively straight. In profile the radial bends below the radial sinus at an angle of 155° between the upper (ambulacral) area and the lower (aboral) portion; at right angles to this the angle between the lateral parts of the plate is approximately 130°. Fine concentric striations occur parallel to the marginal sutures (Plate iv, figure 1).

Specimen B shows a smaller radial plate, the length being 2·5 cm. and width 1·0 cm., the ratio of limbs to body being about 11 to 14. This plate also shows fine concentric ornamentation; it has been somewhat flattened and has cracked across its lower portion (Plate iv, figure 3).

The ambulacra are remarkably narrow, being no more than 2 mm. in width. Specimen A (Pl. iv, fig. 1) shows the position of about 20 small side plates arranged alternately in two rows along the lower part of the ambulacrum. The specimen shows tiny ridges representing the boundaries of the side plates and also the central food groove. The side plates were set at an angle of about 40 degrees with the axis of the ambulacrum. Probably there were at least 40 of these side plates covering the whole length of the lancet plate. The thickening of the lateral ridges into small tubercles near the outer margins of the ambulacrum suggests the former presence of marginal or hydrospire pores between the side plates (Plate iv, fig. 2).

Specimen B does not show the side plates in the ambulacral region, but is the mould of a deeper portion. Two longitudinal grooves (Pl. iv, fig. 3) probably indicate the margins of the lancet plate.

No trace of outer-side plates or any internal structures are present, and no specimens of the basals or deltoids are yet known.

Systematic position.

The distinctive shape of the radial plate, the very narrow ambulacra and the fact that the lancet plate is completely covered by the side plates place it immediately in the family Troostoblastidae (Etheridge and Carpenter, 1886, p. 190), which corresponds with Bather's Series B. Troostoblastida, Family 1. Troostocrinidae (Lankester, 1900, p. 92).

Of the three genera belonging to this family, *Troostocrinus* Shumard, *Metablastus* Etheridge & Carpenter, and *Tricoelocrinus* Meek & Worthen, it appears to be closest to *Tricoelocrinus*, to which it may tentatively be referred in the absence of further details.

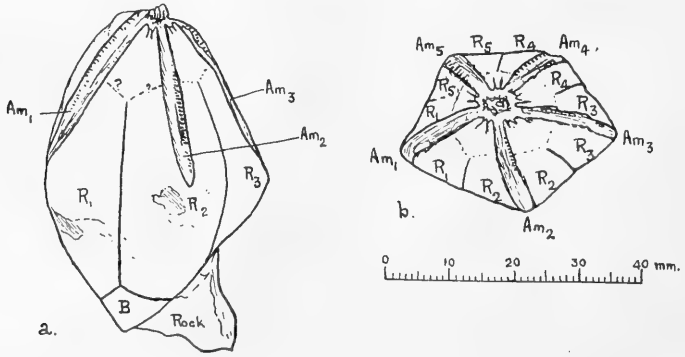
The characters of the radial plate and the ambulacrum distinguish this Blastoid from any described species; we therefore propose for it the name *Tricoelocrinus* (?) *belfordi*, n. sp.

We designate specimen A (39158, Australian Museum Collection) as the type.

Other occurrences.

A specimen of a Blastoid was found by Dr. E. C. Case (see David, 1923, footnote, p. 19) in the Fenestella Shales in the Railway Cutting one mile west of Branxton Railway Station. This locality is three miles to the east of the Belford occurrence. So far as we are aware there is no recorded description of this specimen and its whereabouts is unknown to us. Mr. H. G. Gooch took, for Professor David, a series of 16 photographs of the specimen at the time of its discovery, some of which are reproduced in Plate iv, figures 4, 5, and a plaster cast of this specimen is in the Australian Museum, Sydney. The cast is imperfect and does not show some of the details of the ambulacra, which are clearly visible in the photographs. The accompanying diagram (Text-fig. 1) is based on an examination of the photographs of the original specimen and of the plaster cast.

The specimen is almost complete and is about 5·0 cm. in height; in median cross-section it is sub-pentagonal (Text-fig. 1*b*) and measures 3·3 cm. by 2·2 cm.



Text-figure 1.—Diagrammatic sketch of Blastoid from Branxton, based on plaster cast and photographs of the original specimen (which is now missing). B, basal plate; R_1, R_2, . . . radial plates; Am_1, Am_2 . . . ambulacra.

The calyx shows one of the larger basal plates and five radial plates (which closely resemble those found at Belford). The inter-radial sutures are distinct in the cast and are straight, but the boundaries against the deltoids are obscure. At the tip of each inter-ambulacral area are two small grooves, as shown in the Text-figure. There are five ambulacra, four of which are 3·0 cm. in length, the fifth (Am_5) being 2·5 cm.; the width is fairly uniform, and amounts to 2·5 mm. The photographs show the casts of the (?) side plates, 20 per centimetre occurring on each side of the ambulacrum, indicating about 60 along the whole length of the lancet plate.

The apical parts are not clear; there appears to be a protuberance in the centre of the oral region.

Etheridge (in Jack and Etheridge, 1892, pp. 210–213) described three Blastoids from the Gympie Beds of Rockhampton District, Queensland, which he identified as *Mesoblastus* ? *australis* Eth. fil. (p. 210; Pl. 44, fig. 2), *Granatocrinus* ? *wachsmuthii* Eth. fil. (p. 211; Pl. 7, fig. 10), *Tricoelocrinus* ? *carpenteri* Eth. fil. (p. 212, Pl. 44, fig. 3). These specimens are not available to us for direct comparison, but the description and illustration of *Tricoelocrinus* ? *carpenteri* suggest a close resemblance to the Belford specimen.

In 1906 T. Griffith Taylor described in These PROCEEDINGS, specimens of the radial and basal plates and portions of the ambulacra of a Blastoid collected 2½ miles north of Clarence Town, New South Wales, which he provisionally classed with *Metablastus*. It shows certain resemblances to the specimen under consideration in the size and proportions of the ambulacra and the radial plates, but differs in the arrangement of the side plates and in that the limbs of the radial plate of the Belford specimen are relatively wider.

Geological age.

The Belford specimens come from the Fenestella Shale Bed, which forms part of the Belford 'dome' (Morrison and Jones, 1925, p. 128; Morrison and Raggatt, 1928, p. 111). This horizon is about 1,000 feet below the Muree Rock, and thus occurs in the Branxton Stage of the Upper Marine Series. The upper Marine Series comprises that portion of the Kamilaroi System (David and Sussmilch, 1931, p. 483) whose age is unquestionably Permian; Middle Permian according to David (1932, Table opp. p. 62).

The Rockhampton specimens described by Etheridge come from the 'Gympie Series', an old term, which includes rocks of various ages (Bryan, 1928, p. 33). Some part of the series is equivalent to the Lower Marine Series of the Kamilaroi (David, 1932, Table opp. p. 62) and may be of Permian age and it is probably from these beds that the Blastoids were collected.

The Clarence Town specimens described by Taylor come from the Glenwilliam Beds of the Burindi Series, and are of Lower Carboniferous age.

Permian Blastoids are known from Timor (J. Wanner, 1922, 1924, 1931) and from the Urals (Yakovlev, 1926), but none so far described appears to show any close resemblance to the Australian specimens.

Acknowledgements.

We are indebted to Dr. H. G. Raggatt for informing us of the best collecting grounds in the Fenestella Beds, and to Mr. H. O. Fletcher, of the Australian Museum, Sydney, for the loan of the cast of the Branxton specimen and for his suggestion as to the nature of the partially exposed plate, which was fully

justified on the developing out of the specimen. The photographs of difficult subjects were taken by Mr. H. G. Gooch, of the Department of Geology, Sydney University, to whom our best thanks are due.

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EXPLANATION OF PLATE IV.

Fig. 1.—External mould of radial plate of Blastoid (*Tricoelocrinus* (?) *belfordi*, n. sp.). Showing concentric ornamentation of radial plate and portion of ambulacrum. Locality 2½ miles north of Belford, N.S.W. × 2.

Fig. 2.—Enlargement of ambulacrum given in Fig. 1, showing mould of food groove, side plates and marginal pores. Locality, 2½ miles north of Belford, N.S.W. × 10⅝.

Fig. 3.—External mould of portion of radial plate of *Tricoelocrinus* (?) *belfordi*, showing concentric ornamentation. The ambulacrum shows the position of the lancet plate. Locality, ½ mile west of Belford, N.S.W. × 2.

Fig. 4.—Side view of Blastoid found by Dr. E. C. Case, 1923. The arrangement of the plates is indicated in Text-fig. 1, p. 168. Locality, Railway Cutting, 1 mile west of Branxton, N.S.W. Nat. size.

Fig. 5.—View of the oral surface of Blastoid in Fig. 4, showing arrangement of the ambulacra. Locality, Railway Cutting, 1 mile west of Branxton, N.S.W. Nat. size.

All specimens come from the same horizon, the Fenestella Shales, Upper Marine Series, Permian. Photographs by H. G. Gooch.

TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XV.

THE GENUS RHAGADOCHIR ENDERLEIN, AND GENERA CONVERGENT TO IT.

By Consett Davis, M.Sc., Lecturer in Biology, New England University College.

(Eighty-three Text-figures.)

[Read 27th March, 1940.]

Introduction.

The group of Embioptera whose males have R_{4+5} forked in both wings, the first segment of the left cercus echinulate, the tenth abdominal tergite completely cleft, and, in addition, the process of the left hemitergite complex, forms one of the most difficult in the Order when an attempt is made to frame a natural scheme of classification. Several genera combining the above characters have been dealt with already in this series (*Donaconethis*, *Dihybocercus*, *Odontembia* and *Enveja*). Apart from the species contained in these genera, it has been the current practice to place any species with the above combination of characters in the genus *Rhagadochir* Enderlein 1912. To continue on this course would be to allow a large number of ill-assorted forms to be brought together in one genus, which would act in effect as a dumping-ground for species not referable to other already-known genera. This results largely from the fact that the complexity of the process of the left hemitergite is a character which tends to arise frequently by convergence (Davis, 1938); it is found in such unrelated genera as *Oligotoma* and *Metoligotoma*, in addition to the four genera listed above, and the genera discussed in this paper.

The course here adopted, namely, the splitting-off of a number of small genera, seems to be the only possible one having due regard to geographic as well as structural facts. The greatest difficulty lies in the separation from *Rhagadochir* of its Neotropical parallels; indeed, the only entirely satisfactory key separating these series would be geographic, not structural. This does not imply, however, that a genus truly common to both sides of the Atlantic has been split arbitrarily into two units.

The fact that the type of Embiopteron with the process of the left hemitergite simple, such as is presumably to be considered as ancestral to the insects under discussion here, has no genus common to the two sides of the Atlantic, gives weight to the consideration that the Neotropical species with this process bifid should be separated generically from their African parallels, and considered as closely convergent rather than closely related. Granted this point, the subdivision of the African species into five genera (including *Rhagadochir*) is a natural corollary, as the structural differences of these five genera *inter se* are greater than those between some of them and the Neotropical series.

Against the charge that this course involves an orgy of generic splitting and a number of monotypic genera, it may be noted that the author has refrained

from splitting either *Oligotoma* or *Metoligotoma*, even into subgenera, on the complexity of the process of the left hemitergite; this convergent character, taken alone, could not justify the subdivision of an otherwise homogeneous array.

A truer perspective on the merits and demerits of the present course should result from the collection of further species, especially in Africa; this may also enlarge the concepts of some of the smaller genera, and terminate their monotypic state.

The difficulties of the present paper have not been lightened by the fact that Enderlein's description of the genotype, *Rhagadochir vosseleri*, omits some very important details (number of tarsal bladders, structure of inner process of right hemitergite and of the ventral parts of the terminalia).

Genus Rhagadochir Enderlein 1912.

Coll. zool. de Selys-Longchamps, fasc. 3, p. 54. Genotype, *Embia vosseleri* Enderlein, 1909, *Zool. Anz.*, Bd. 35, p. 181.

The genus may be delimited as follows: African Embioptera, the males with the following characters: Winged, the veins fairly well developed; R_{4+5} forked, the fork longer than the stem; M and Cu_{1a} simple, rather weak. Hind tarsi with two rather small bladders ventrally on the first segment. Tenth abdominal tergite completely divided; right hemitergite with a terminal process directed downwards, sharp or bifid; process of left hemitergite with a lateral lobe or flap. First segment of left cercus strongly clavate, echinulate. Right cercus-basipodite small.

The structure of the hind tarsus and right cercus-basipodite, not mentioned in Enderlein's description of the genotype, is assumed to be the same as in the two new species described below, which are fairly closely related to *Rh. vosseleri*, and from the same region.

Rhagadochir vosseleri Enderlein (1909). Figs. 1–2.

Embia vossleri Enderlein 1909, l.c.—*Rhagadochir vosseleri* Enderlein, 1912, l.c. (Named after Professor Vosseler; Enderlein's original spelling 'vossleri' may be regarded as a lapsus calami. It has been corrected by Krauss (1911) and Enderlein himself (1912), and the amended spelling may be adopted.)

♂ (after Enderlein, 1909, 1912). Length 9¼ mm.; forewing 9½ mm., hindwing 8½ mm. Head, pronotum, legs and abdomen pale rusty-yellow, thorax pale yellowish-brown, metatarsus of the forelegs more brownish. Eyes and antennae black. Pubescence of antennae brown, of body and legs yellowish. Wings brown, pseudo-radial lines reddish-brown, veins dark brown, inter-venal lines colourless. Venation and terminalia as in figures 1–2 (after Enderlein, 1912).

♀ unknown.

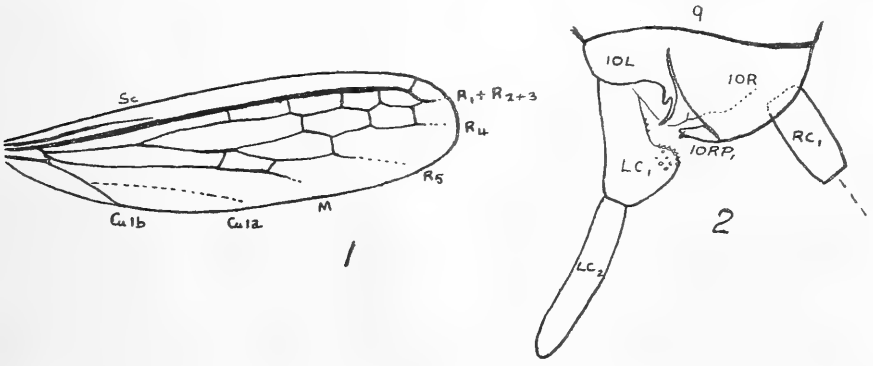
Locality.—Amani, Tanganyika (type in Berlin Zool. Museum).

The type requires re-examination. Enderlein does not give the number of bladders on the hind metatarsus, but related species described below have two. The tenth abdominal tergite is shown as incompletely split in Enderlein's figure, but this is almost certainly inaccurate. Fuller details of the processes of the hemitergites, and information concerning the ventral structures, would be desirable.

The data given by Friederichs (1934, p. 408, fig. 1*b*) do not refer to the type, nor do they do much to clarify the situation. His specimen, of which the exact locality is not given, is probably not conspecific with Enderlein's type.

RHAGADOCHIR CARPENTERI, n. sp. Figs. 3–12.

♂. Length 8 mm.; forewing 6·2 mm. × 1·4 mm.; hindwing 5·8 mm. × 1·4 mm.; head 1·3 mm. × 1·0 mm. General colour chocolate-brown, head dark brown, eyes black; wing-veins dark brown, bands mid-brown. Head (Fig. 3) with large prominent eyes, sides behind eyes converging posteriorly. Antennae incomplete; mandibles (Fig. 4) with acute terminal and subterminal teeth, the left with three, the right with two, incurved. Wings (Fig. 5) with fork of R_{4+5} longer than stem; most of R_5, M, and Cu_{1a} obsolescent. Hind tarsi (Fig. 6) with two small ventral bladders on first segment, one on second. Terminalia (Figs. 7–12) with tenth tergite completely cleft, hemitergites widely separated by more or less membraneous areas; right hemitergite (10R) produced backward and to the right into an acute, slender spine ($10RP_1$), directed downward. Inner margin of 10R



Figs. 1-2*.—*Rhagadochir vosseleri* Enderlein, ♂. 1. Right forewing, × 6. 2. Terminalia from above, × 30. (After Enderlein, 1912.)

produced forward as a chitinous rod ($10RP_2$). Lying between the hemitergites is a membraneous flap, obtusely tapered, directed downward; it is chitinized medially, the chitinization apparently originating at the terminal part of $10RP_2$. Left hemitergite (10L) curved backward from inner margin as a complex process (10LP) (Figs. 8–9), the inner margin of which continues backward as a slender, acute spine curved outward, the outer margin as a broad, obtuse process, more dorsal in position, and less heavily sclerotized. First segment of right cercus (RC_1) subcylindrical, arising from a small annular basipodite (RCB); second segment missing, but undoubtedly subcylindrical. First segment of left cercus (LC_1) distally produced inward to a rather slender echinulate lobe; second segment subcylindrical. Hypandrium (H) produced backward into an obtuse process (HP) to the right of the mid-line; left cercus-basipodite (LCB), situated between HP and base of LC_1, laminoid, distally produced into a subacute hook curving to the right and underlying the tip of HP.

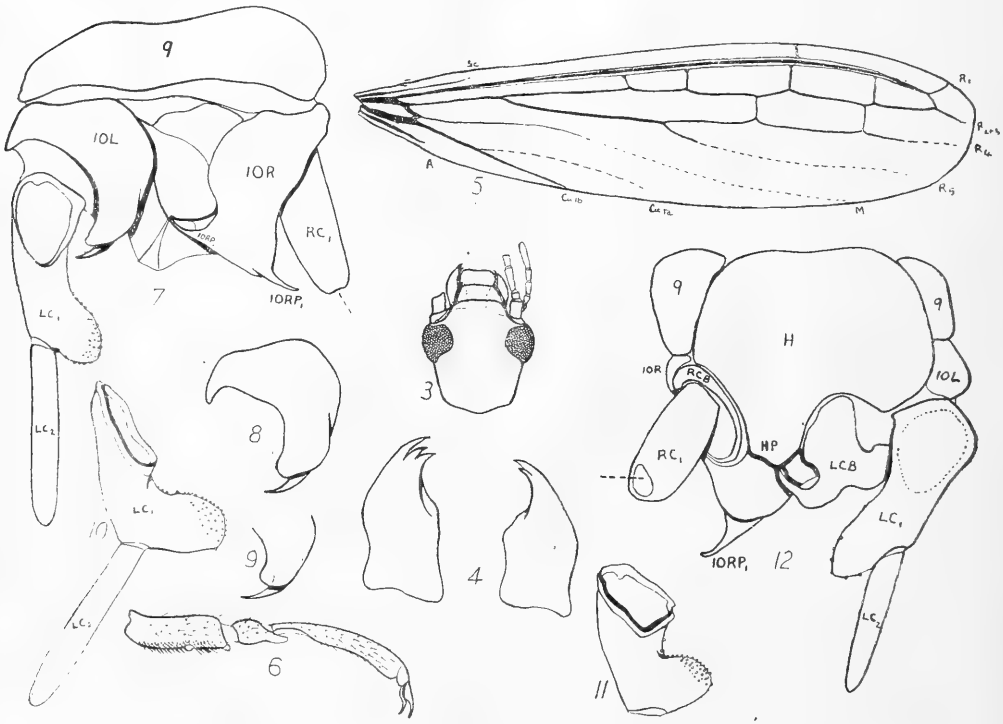
♀ unknown.

* Conventional lettering for venation. 9, ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; $10RP_1$, $10RP_2$, posterior and inner processes of 10R; 10LP, process of 10L; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; H, ninth abdominal sternite; HP, process of H.

Original figures all based on camera lucida outlines, except Figures 24-28, 51-57, and 67-69, which were prepared with constant reference to an ocular micrometer. Setae omitted except in Figures 6, 26, 51, and 77.

Locality.—Lulanguru, Tanganyika, November 1917, coll. Dr. G. D. Hale Carpenter, after whom the species is named. Holotype ♂ in the British Museum of Natural History.

The great structural similarity to the Neotropical species is discussed later. The erection of a new species on a single specimen may appear unwise, but it is considered as justified by the morphological and geographic interest of the specimen; considering both structure and locality, it is the most problematical specimen handled by the writer, so that omission of the details would be unpardonable. Moreover, the taxonomic characters are clear, and the exact locality is stated on the museum label.



Figs. 3-12.—*Rhagadochir carpenteri*, n. sp., holotype ♂. 3. Head from above, × 15. 4. Mandibles from above, × 45. 5. Right hindwing, × 15. 6. Hind tarsus viewed laterally, × 45. 7. Terminalia from above, × 45 (left cercus in unnatural position). 8. Left hemitergite from above, × 45. 9. Process of left hemitergite, viewed more from behind than in Fig. 8, × 45. 10. Left cercus from above, × 45. 11. First segment of left cercus viewed laterodorsally from the right, × 45. 12. Terminalia from below, × 45, left cercus in unnatural position.

RHAGADOCHIR BEAUXII, n. sp. Figs. 13–17.

♂. Length 11 mm.; head 2·4 mm. × 1·9 mm. General colour dark golden-brown, pronotum and legs orange-yellow, head and antennae dark brown, eyes black, clypeus orange-brown. Wing-veins dark brown, bordered by bands of medium smoky-brown, lines between bands hyaline. Head (Fig. 13) similar in general form to *Rh. carpenteri*, the eyes relatively smaller. Antennae incomplete. Wings as in *Rh. vosseleri*. Tarsi as in *Rh. carpenteri*. Terminalia (Figs. 14–17) with

tenth abdominal tergite completely divided; posterior process of right hemitergite ($10RP_1$) simple, short and acute, directed inward and downward; inner process ($10RP_2$) subacute behind, in front contorted. Left hemitergite (10L) with its process (10LP) bifid, the main lobe acute, terminally directed downward and to the left; lateral process of 10LP flap-like, with its free edge rounded, directed upward, backward and to the right (Figs. 15, 16). Left cercus with inner margin of first segment (LC_1) produced inward in a prominent, rounded, echinulate lobe, nearer to apex than to base; second segment (LC_2) subcylindrical. Ventral structures (Fig. 17) as in *Rh. carpenteri*, but with the process of the left cercus-basipodite tapered, sinuous and acute, directed backward.

♀ unknown.

Locality.—Kabulamuliro, Uganda, vi.1916, Dre. E. Bayon. Holotype ♂ in Museo Civico di Storia Naturale, Genoa. Dedicated to Dre. Oscar de Beaux, Director of the above Museum.

Key to the Species of Rhagadochir (♂).

1. Posterior process of right hemitergite of tenth abdominal segment simple 2
   Posterior process of right hemitergite bifid ..... *vosseleri* Enderlein.
2. Left cercus-basipodite with a subacute process curving to the right under the hypandrium ..... *carpenteri*, n. sp.
   Left cercus-basipodite tapered backwards to a sinuous, subacute process .... *beauxii*, n. sp.

Note.—The type (♂) of *Embia* (*Rhagadochir*) *chudeaui* Navás 1922, *Rev. Acad. Cienc. Zaragoza*, vii, p. 29 (Mus. Paris), proved on examination to have the process of the left hemitergite simple. It is a normal species of *Embia* Latreille in the strictest sense, and will be dealt with under that genus. It is no relation to *Rhagadochir* in any sense.

Genus Chirembia, n. gen.

Genotype, *Embia xanthocera* Navás, 1930, *Ann. Mus. Civico di Storia Naturale, Genoa*, vol. 55, p. 152, fig. 4.

African Embioptera, the males with the following characters: Winged, with R_{4+5} forked, the fork longer than the stem; M and Cu_{1a} simple, weak; cross-veins few. Hind tarsi with only the terminal ventral bladder present. Tenth abdominal tergite completely divided; right hemitergite with an elongate posterior process curved downward, and an inner flap-like process similar to that in *Embia* Latreille. Process of left hemitergite bifid, with a distinct distal concavity between the lobes. First segment of left cercus produced inward distally into a prominent echinulate beak.

The differentiation from other genera is summarized in the generic key (infra). The genus is derivable from *Embia* by the elongation of the posterior process of the right hemitergite, the forking of the process of the left hemitergite, the excessive curvature of the first segment of the left cercus, and the weakening of the venation.

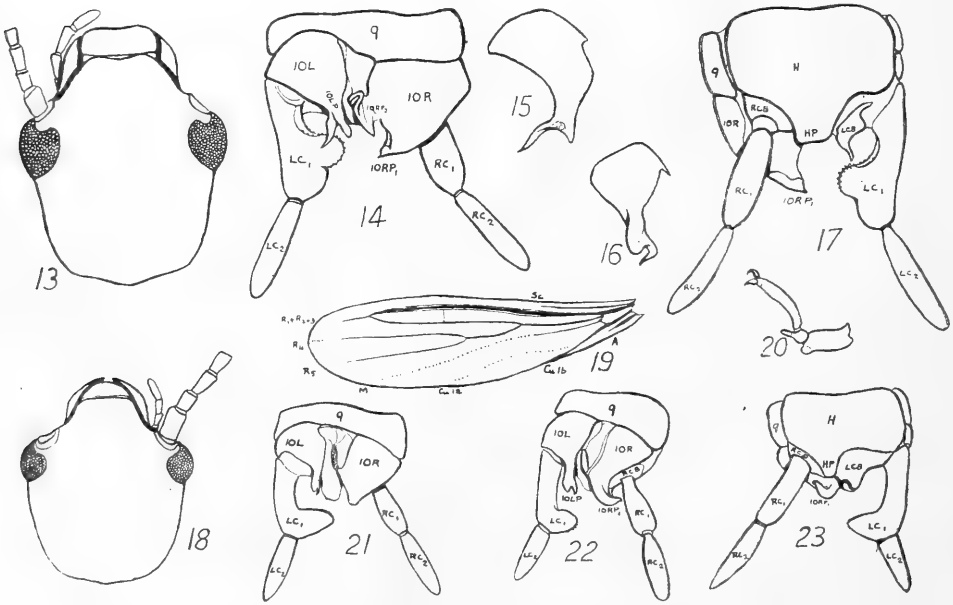
Chirembia xanthocera (Navás 1930). Figs. 18–23.

Embia xanthocera Navás 1930, l.c.

The following re-description is from the unique type (Mus. Genoa):

♂. Length 7·2 mm.; head 1·4 mm. × 1·2 mm.; forewing 5·5 mm. × 1·5 mm.; hindwing 4·5 mm. × 1·5 mm. General colour dark brown, head paler, ferruginous, eyes black, antennae yellowish-brown; wing-veins dark brown, bordered by mid-brown bands, lines between bands hyaline. Head (Fig. 18) with eyes rather small,

sides behind eyes converging slightly, smoothly rounded behind. Antennae incomplete. Wings (Fig. 19) with veins distributed as in *Rh. vosseleri*, but with very few cross-veins, and with a general weakening of the main veins; M distinct only for a short distance basally, thence represented by a row of macrotrichia and by bordering pigment-bands. Cu_{1a} represented only by macrotrichia and pigment-bands, which in both right wings are divided by an oblique hyaline line. The other veins, except the stem of the cubitus (Cu_{1b}), fail to reach the wing margin, although their continuations (as rows of macrotrichia) do so. Hind tarsi (Fig. 20) with only the terminal bladder present on the first segment, remainder of ventral surface of this segment clothed with setae, as in *Embia*. Terminalia (Figs. 21–23) with tenth abdominal tergite completely divided longitudinally, the right hemitergite (10R) tapered backward to a process ($10RP_1$), curving down and a little to the right, and terminally directed forward. Inner margin of 10R with a flat bar of chitin ($10RP_2$), as in *Embia*, separated from 10R by membrane except at posterior limit. Left hemitergite (10L) with inner margin produced back to an acute process (10LP), curved slightly to the left terminally; a flat lobe arises subterminally from the left of this process, directed laterodorsally to the left, with the outer margin roughened. Right cercus with two subequal subcylindrical segments (RC_1, RC_2), arising from a subannular cercus-basipodite (RCB). Left cercus with first segment (LC_1) strongly incurved apically to a long echinulate



Figs. 13-17.—*Rhagadochir beauxii*, n. sp., holotype ♂. 13. Head from above, × 15. 14. Terminalia from above, × 20. 15. Left hemitergite of tenth abdominal segment, viewed from above and to the left, × 20. 16. Left hemitergite viewed from above and to the right, × 20. 17. Terminalia from below, × 20.

Figs. 18-23.—*Chirembia xanthocera* (Navás), holotype ♂. 18. Head from above, × 20. 19. Left forewing, × 8. 20. Hind tarsus viewed laterally, × 20. 21. Terminalia from above, × 20. 22. Terminalia from above and to the right, × 20. 23. Terminalia from below, × 20.

beak; second segment (LC_2) short, subcylindrical. Ninth sternite (H; fig. 23) produced backward to the right of the mid-line in a short obtuse lobe (HP), to the left of which is a concavity filled by the left cercus-basipodite (LCB); the latter is produced back to a flat obtuse lobe, curving downward terminally.

♀ unknown.

Locality.—Gaharre (or Gaarre), Dancalia (= Danakil, Ethiopia), xii.1929, Franchetti Expedition. Type in Mus. Genoa.

Genus Navásiella, n. gen.

Genotype, *Oligotoma sulcata* Navás, 1923, *Rev. Acad. Cienc. Zaragoza*, viii, p. 16.

Rather small African Embioptera, the males with the following characters: Winged, veins weak, R_{4+5} forked, the veins distad to the fork subobsolescent; M and Cu_{1a} simple, obsolescent. Hind tarsi with a large terminal bladder ventrally on the first segment, and a small bladder medially on the ventral surface of this segment. Tenth abdominal tergite completely divided longitudinally; right hemitergite as in *Embia*, with a short acute posterior process and a flap-like inner process. Process of left hemitergite acute, with a flat lobe subterminally on the left, not separated from the main process by a deep concavity. First segment of left cercus produced inward in a long echinulate lobe or beak, directed slightly forward.

Differs from *Chirembia* in the hind tarsi, weaker venation, and in the structure of the posterior process of the right hemitergite and of the process of the left hemitergite. Resembles *Embia* more closely than does *Chirembia* in the structure of the hemitergites, but differs more from *Embia* than does *Chirembia* in the tarsi, wings, and left cercus.

Navásiella sulcata (Navás 1923). Figs. 24–28.

Oligotoma sulcata Navás 1923, l.c.

The following re-description is from the unique type (Mus. Paris):

♂. Length 7 mm.; head 1·3 mm. × 1·1 mm.; forewing 4·2 mm. × 1·2 mm.; hindwing 3·8 mm. × 1·1 mm. General colour very dark brown, with white pubescence; wings smoky-brown with hyaline streaks longitudinally. Head (Fig. 24) and thoracic scuta minutely rugose; head broad, sides behind eyes converging only slightly; eyes small. Wings (Fig. 25) as in generic description, R_{4+5} distad to fork, M, and Cu_{1a}, represented only by rows of macrotrichia and bordering pigment-bands. Hind tarsi (Fig. 26) as in generic description. Terminalia (Figs. 27–28) with posterior process of right hemitergite ($10RP_1$) short, acute, directed inward and downward; inner process ($10RP_2$) subelliptical, continuous with right hemitergite (10R) posteriorly, anteriorly separated by membrane. Process of left hemitergite (10LP) acute, subterminal flap obtusely rounded, directed to the left. First segment of left cercus (LC_1) strongly incurved to a long process, directed slightly forward, terminally echinulate; second segment lacking in the type. Hypandrium (H) produced back to an obtusely-tapered process (HP) to the right of the mid-line; left cercus-basipodite (LCB) produced back to an obtuse lobe on the left of HP; left-hand margin of LCB furrowed longitudinally. Right cercus composed of two subcylindrical segments (RC_1, RC_2); right cercus-basipodite (RCB) small, subannular.

♀ unknown.

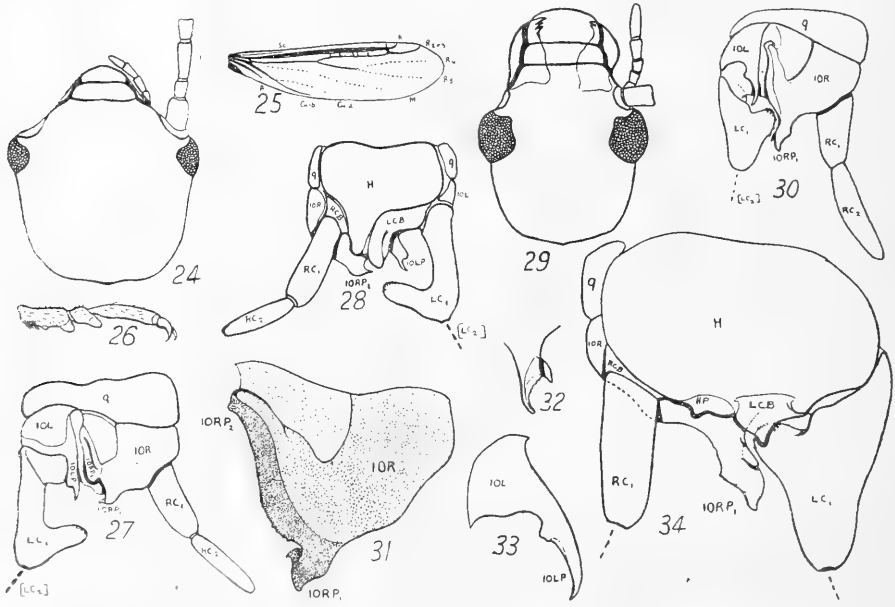
Locality.—Africa: Galla Annia, Gobele, vi.1903, Mission du Bourg de Bozas.

Genus Parachirembia, n. gen.

Genotype, *Embia* (*Rhagadochir*) *apicata* Silvestri 1921, *Trans. Ent. Soc. London*, p. 449, Pl. ix, x.

Medium-sized African Embioptera, the males with the following characters: Winged, R_{4+5} forked, the fork longer than the stem; M and Cu_{1a} simple; all veins well developed. Hind tarsi with only the terminal bladder on the first segment. Tenth abdominal tergite completely cleft longitudinally; right hemitergite produced backward to a bifid process; inner margin of right hemitergite produced forward towards ninth tergite as a chitinous rod. Process of left hemitergite acute, with a small protuberance on the left-hand margin near origin from hemitergite. First segment of left cercus clavate, internal lobe strong, echinulate, directed slightly forward. Right cercus-basipodite small.

The differences from other genera are shown in the generic key (infra). The closest genus structurally seems to be *Chirembia*, which has the hemitergites of different form, and the venation weaker.



Figs. 24-28.—*Navásiella sulcata* (Navás), holotype ♂. 24. Head from above, × 23. 25. Right forewing, × 6⅔. 26. Hind tarsus viewed laterally, × 23. 27. Terminalia from above, × 23. 28. Terminalia from below, × 23.

Figs. 29-34.—*Parachirembia apicata* (Silvestri), ♂ (plesiotype). 29. Head from above, × 17. 30. Terminalia from above, × 17. 31. Right hemitergite of tenth abdominal segment viewed from above, × 33. 32. Extremity of right hemitergite, viewed from the right and somewhat below, × 33. 33. Left hemitergite from above, × 33. 34. Terminalia from below, × 33.

Parachirembia apicata (Silvestri 1921). Figs. 29–34.

Embia (*Rhagadochir*) *apicata* Silvestri 1921, l.c.

Silvestri's excellent description is based on specimens from Agege, near Lagos, coll. C. O. Farquharson, from the bark of the Pará rubber tree (v. *Trans. Ent. Soc. London*, 1921, pp. 413–416, for details of the habitat). Two males in the British

Museum are labelled 'Southern Nigeria, C. O. Farquharson: 1915—116', and a piece of web, bearing the same label and museum number, has the additional data 'Web of Embiidae from Pará tree'. These males are evidently members of the series, others of which formed Silvestri's types. They agree exactly with Silvestri's description. The accompanying description and figures are from one of these, which has been labelled plesiotype.

♂. Length 10·5 mm.; head, length 1·9–2·0 mm., breadth 1·4–1·6 mm.; forewing 10·3 mm. × 3·0 mm. General colour dark brown, thoracic nota pale yellowish-brown, eyes black; wing-veins dark brown, bordered by bands of medium smoky-brown, lines between bands hyaline Head (Fig. 29) similar in outline to *Rh. beauxii*; left mandible with three acute incurved teeth terminally, right with two. Wings as in generic description (v. Silvestri, l.c., figs. 1–2). Hind tarsi with first segment furnished with only the terminal bladder (v. Silvestri, l.c., fig. 6). Terminalia (Figs. 30–34) with tenth abdominal tergite completely cleft, right hemitergite (10R) produced backward, inward and downward to a long process ($10RP_1$), irregularly tapered, apex directed outward, subobtuse, with a subterminal ventral tooth arising from the left side and curving downward (Figs. 31–32). Inner margin of right hemitergite heavily sclerotized, forming a forwardly-directed process ($10RP_2$) not quite reaching the posterior border of the ninth tergite; free edge of $10RP_2$ slightly echinulate posteriorly. Left hemitergite (10L) with inner margin produced back to a slender process (10LP), terminally falciform-acute, directed to left, with a very short, blunt lateral lobe near the base directed to the left (Fig. 33). Right cercus with two subequal subcylindrical segments (RC_1, RC_2), with a vestigial cercus-basipodite (RCB). Left cercus with first segment (LC_1) clavate, the middle of the inner margin produced inward and forward to a large rounded echinulate lobe; second segment missing in specimens seen by the writer, but according to Silvestri's figures (l.c., figs. 7, 8) simple, subcylindrical. Ninth sternite (H; fig. 34) with right-hand part of distal margin carrying a small blunt process (HP), heavily sclerotized; left cercus-basipodite (LCB) fused distally to the left side of H, heavily sclerotized, produced backward to a blunt, papillose end.

♀. Silvestri (l.c.) has described the female. As is the case throughout the Order, it is of little taxonomic importance.

Locality.—Agege, near Lagos, Nigeria. Plesiotype ♂ in the British Museum.

Genus Macrembia, n. gen.

Genotype, *Embia lunaris* Navás 1926, *Mem. Pont. Accad. delle Scienze, Nuovi Lincei*, Series ii, vol. 9, p. 108.

Medium-sized African Embioptera, the males with the following characters: Winged, R_{4+5} forked, the fork longer than the stem; M and Cu_{1a} simple; all veins well-developed, cross-veins numerous. Hind tarsi with two large ventral bladders on first segment, one on second. Tenth abdominal tergite completely divided longitudinally; right hemitergite with a short posterior process directed inward, and a flap-like inner process, as in *Embia*. Process of left hemitergite bifid, with a deep distal concavity between its lobes. Right cercus-basipodite relatively large, produced to the left.

The right hemitergite and its processes agree with *Embia* Latr., from which *Macrembia* is differentiated by the left hemitergite, right cercus-basipodite, hind tarsi, etc. The left cercus agrees with *Parachirembia*, but the hemitergites and their processes, the right cercus-basipodite, and the tarsi, differentiate it completely.

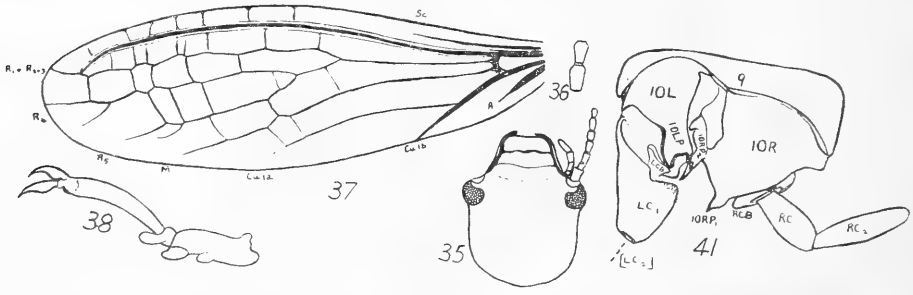
Macrembia differs from *Rhagadochir* in the right cercus-basipodite, and in the strength of development of the venation and tarsal bladders; it differs from *Dihybocercus* End. in the form of the left cercus and right cercus-basipodite, and in the branching of the cubitus, but is in some respects rather closely related.

MACREMBIA LUNARIS (Navás 1926). Figs. 35–41.

Embia lunaris Navás 1926, l.c.

Navás' description contains little of taxonomic importance. He named two types, one (the first-named) being lodged in the Musée du Congo, Tervueren. The following description and figures are from this specimen, which may be regarded as the holotype (lectotype):

♂. Length 12 mm.; head 3·0 mm. × 2·5 mm.; forewing 10 mm. × 3 mm.; hindwing 9 mm. × 3 mm. General colour dark brown, pronotum and posterior part of head orange-brown, wing-veins dark brown, bordered by mid-brown pigment-bands, between which are hyaline lines. Head (Fig. 35) large, sides behind eyes not converging, but smoothly rounded posteriorly. Left antenna incomplete, right with 29 short segments (Fig. 36), total length 3 mm. Wings with numerous cross-veins, all veins strong, R_{4+5} with fork twice length of stem, cubitus two-branched. The left forewing (Fig. 37) shows a venational anomaly, in that the stem of R_{4+5}, before the fork, is very short, and both R_4 and R_5 are shortly bifid terminally. Hind tarsi (Fig. 38) with two large ventral bladders on first segment, one on second. Terminalia (Figs. 39–40) with tenth abdominal tergite completely



Figs. 35-40.—*Macrembia lunaris* (Navás), holotype ♂. 35. Head from above, × 7. 36. Two of distalia, × 17. 37. Left forewing, showing venational aberration (R_4 and R_5 both forked), × 7. 38. Hind tarsus viewed laterally, × 17. 39. Terminalia from above, × 17. 40. Terminalia from below, × 17.

Fig. 41.—*Macrembia lunaris* (Navás), ♂, aberrant specimen from Northern Rhodesia. Terminalia from above, × 17.

divided longitudinally; right hemitergite (10R) posteriorly produced downward and inward to a simple process ($10RP_1$), short and acute; inner margin of 10R with a flat sclerotized strip or flap ($10RP_2$), separated from body of 10R, except at posterior limit, by membraneous areas. Anteriorly, $10RP_2$ has a small accessory lobe, rounded and weakly rugose. Left hemitergite (10L) with inner margin produced back to a process (10LP), elongate, acute, terminally curved slightly to the left, with a flat lateral lobe, placed more dorsally, on the left-hand side, directed backward; concavity between lobe and main process echinulate. Right cercus with two subcylindrical segments, the first (RC_1) slender at the base, where it arises from the large cercus-basipodite (RCB), the second (RC_2) slightly longer and thicker. Left cercus with first segment (LC_1) produced inward to an echinulate lobe directed forward, second segment (LC_2) subcylindrical. Ninth sternite (H) and left cercus-basipodite (LCB) much as in *Parachirembia apicata*, the terminal process of H less prominent.

Locality (of lectotype).—Elisabethville (R. Lubumbashi), Congo, 1920, Dr. Bequaert (Mus. Congo).

A specimen (♂) in the British Museum of Natural History, from Northern Rhodesia (Congo Border: Tutivi Pt., 15 miles east of Kipushi; 25/11/1927, H. Silvester Evans), is referable to this species, but has slight variations in the terminalia (Fig. 41). The left cercus-basipodite is acute, directed to the left; the concavity between the lobes of the process of the left hemitergite, and the anterior part of the inner process of the right hemitergite, are smooth. In all other respects, including colour and size, this specimen agrees with the lectotype.

Genus Pararhagadochir, n. gen.

Genotype, *Embia trinitatis* de Saussure, 1896, *Journ. Trinidad Club* (Port of Spain), vol. 2, no. 12, p. 293.

Medium-sized to rather small Neotropical Embioptera, the males with the following characters: Winged, R_{4+5} forked in both wings, M and Cu_{1a} simple, veins rather weakly developed, obsolescent terminally. Hind tarsi with first segment carrying a terminal ventral bladder; medial bladder not apparent except in one species, where the extra bladder appears to be a constant character. Tenth abdominal tergite completely cleft longitudinally; right hemitergite produced backward and downward to a process, acute or weakly bifid; inner margin of right hemitergite produced forward towards ninth tergite as a sclerotized rod; space between this process and left hemitergite occupied by an obtuse membraneous flap directed downward and backward, with a medial chitinization connecting to the end of the inner process of the right hemitergite. Process of left hemitergite strongly bilobed; right lobe acute, separated from left lobe by a deep concavity; left lobe broader, obtuse, flattened, less heavily sclerotized. First segment of left cercus clavate, echinulate.

In specimens of only one South American species, with the above combination of characters, seen by the writer, was the second or medial ventral bladder present on the hind metatarsus. In one additional case, the sclerotization and pigmentation of the area where this additional bladder occurs in other genera was weaker, although no projection of this area of weakness occurred. In one species, however, (infra) the extra bladder was constantly present. It seems necessary to assume temporarily that a single hind metatarsal bladder is characteristic of this series (genus), two occurring in only one aberrant series (species).

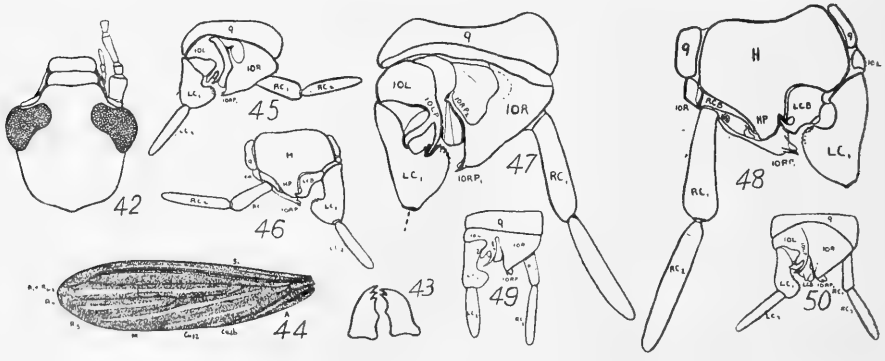
The terminalia of this series are not generically separable from the East African species *Rhagadochir carpenteri*, although they are not very closely related to *Rh. beauxii*, nor, probably, to *Rh. vosseleri* End., of which full details are lacking. The unique specimen of *Rh. carpenteri* has two hind metatarsal bladders (Fig. 6). Discarding the attractive theory that the problem of *Rh. carpenteri* is to be explained by the transposition of museum labels at some time, and that it is in reality Neotropical, we must assume that this species represents an amazingly close case of convergence, the terminalia of the end product being indistinguishable generically from the Neotropical species, though possibly reached by a different sequence of evolutionary steps. On the concept advanced earlier (Davis, 1938, p. 268 et seq.), this is not impossible. The fact that *Rh. carpenteri* is from East Africa is significant; the known West African species (of *Parachirembia*, *Macrembia*, etc.) are much further removed from the Neotropical species.

PARARHAGADOCHIR TRINITATIS (de Saussure 1896). Figs. 42–48.

Embia trinitatis de Saussure, 1896*a*, *Journ. Trinidad Club*, vol. 2, no. 12, p. 293; de Saussure, 1896*b*, *Mitt. Schweiz. Entomol. Gesellschaft*, Bd. 9, Hft. 8, p. 352.

The following re-description is from one of de Saussure's cotypes (♂; Mus. Geneva); this was a dried specimen, which was macerated and cleared. The type locality was given as Trinidad; the detailed locality is probably Port of Spain, where Urich, the collector, was then stationed. The description is supplemented from a well-preserved (alcoholic) male from St. Augustine, Trinidad (coll. N. A. Weber, 10.5.35; Museum of Comparative Zoology, Harvard University). The specimens seem to agree exactly; certain figures of the St. Augustine specimen are given, in addition to those of the cotype, as some structures are much clearer in the former.

♂. Length (after de Saussure, 1896*a*, *b*) 7–8 mm.; length of forewing 7 mm. The dimensions of the cotype seen by me are: Length 8 mm.; head 1·3 mm. × 1·0 mm.; forewing 5·2 mm. × 1·4 mm.; hindwing 4·8 mm. × 1·5 mm. The



Figs. 42-46.—*Pararhagadochir trinitatis* (Sauss.), cotype ♂. 42. Head from above, × 17. 43. Mandibles from above, × 17. 44. Left forewing, × 7. 45. Terminalia from above, × 17. 46. Terminalia from below, × 17.

Figs. 47-48.—*Pararhagadochir trinitatis* (Sauss.), ♂, St. Augustine, Trinidad. 47. Terminalia from above, × 33. 48. Terminalia from below, × 33.

Figs. 49-50.—*Pararhagadochir flavicollis* (Enderlein). 49. ♂ from Venezuela (type), terminalia from above, × 11. 50. ♂ from Bolivia (type), terminalia from above, × 11. (After Enderlein, 1912, figs. 29, 30.)

dimensions of the St. Augustine specimen are: Length 7·5 mm.; head 1·2 mm. × 0·9 mm.; forewing 6·4 mm. × 1·6 mm.; hindwing 5·2 mm. × 1·6 mm. General colour of alcoholic specimen dark brown, head very dark, eyes black; wings with mid-brown veins and rather pale brown longitudinal bands, hyaline inter-venal lines narrow; prothorax cream (in the dried cotype, much darker, orange, still very distinct, however, from the general body-colour). Head (Fig. 42) relatively broad, eyes very large; sides behind eyes clearly convergent posteriorly. Antennae incomplete in the cotype; in the St. Augustine specimen, left broken, right with 23 segments, total length 4 mm. (de Saussure, l.c., gives 21–22 segments). Mandibles (Fig. 43) incurved, the left with three, the right with two acute teeth. Wings (Fig. 44) as in generic description; cross-veins few (in the St. Augustine specimen, more cross-veins are present than in Figure 44, from the cotype: R_1–R_{2+3} (1), R_{2+3}–R_4 (2), and traces of three between R_1 and the costa). R_5 distinct only at base, M and Cu_{1a} scarcely at all; veins, when subobsolescent, represented, as elsewhere, by rows of macrotrichia and by the bordering pigment-bands. Hind tarsi with only the terminal bladder present on the first segment. Terminalia (Figs. 45–46, cotype; Figs. 47–48, St. Augustine specimen) with tenth abdominal tergite completely cleft; right hemitergite (10R) subtriangular, inner margin with a basal membraneous concavity, distally repesented as a sclerotized rod ($10RP_2$), projecting forward towards ninth tergite. Posteriorly, 10R is produced backward and downward into a heavily-sclerotized, acute process ($10RP_1$), with a small obtuse subterminal lobe, placed ventrally and projecting to the left. Median membraneous flap as in *Rhagadochir carpenteri*. Process of left hemitergite (10LP) bifid, inner lobe slender, acute, curved to the left, outer lobe slender, sinuous, subobtuse, less heavily sclerotized. Left cercus with first segment (LC_1) clavate, inner lobe large, subterminal, directed slightly forward, distally echinulate; second segment (LC_2) slender, subcylindrical. Right cercus composed of two elongate subcylindrical segments (RC_1, RC_2), the first somewhat dilated distally; right cercus-basipodite (RCB) small, with a trace of an extra distal sclerite, as in *Clothoda urichi* (Sauss.). Hypandrium (H) produced into an obtuse lobe (HP) to the right of the mid-line; concavity to the left of HP occupied by laminoid left cercus-basipodite (LCB), which is produced as an incurved spine underlying the tip of HP, as in *Rhagadochir carpenteri*.

♀. See de Saussure (1896*a*, *b*). The colour of the dried ♀ cotype seen by the writer agreed with that of the dried ♂, from which it may be assumed that the pronotum is cream in living or alcoholic material.

Note.—Krauss (1911, p. 42) incorrectly refers this specimen to *Oligotoma*. Enderlein (1912, p. 30) refers to *Embia trinitatensis* Sauss., a lapsus calami for *trinitatis*.

PARARHAGADOCHIR FLAVICOLLIS (Enderlein 1909). Figs. 49–50.

Embia flavicollis Enderlein 1909, *Zool. Anz.*, Bd. 35, p. 184.—*Rhagadochir flavicollis* Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 56, figs. 29, 30.

This species is closely related to *P. trinitatis* (Sauss.), in size (length 6·5–8 mm.; length of forewing 6–6·5 mm., of hindwing 5·3–6 mm.), colour (exactly similar), venation (similar, but with more cross-veins), and form of the male terminalia. It will probably prove to be distinct only subspecifically. Enderlein (1912) figures and describes two males (the types; Mus. Stettin), one from Bolivia, one from Venezuela; the former is cited first in the text (1909, 1912), the latter figured first (1912); the former should probably be called the

holotype. Enderlein's figures of the terminalia (dorsal view only) cannot be regarded as entirely accurate, as the tenth abdominal tergite is shown as incompletely split; however, drawing a comparison between these figures and *P. trinitatis*, the following details may be noted:

(1). The posterior process of the right hemitergite ($10RP_1$) is out-curved. It seems to resemble that of *P. trinitatis* in its component parts, having a sharp spine and an obtuse lobe; whether the latter is membraneous cannot be decided from Enderlein's verbal description or line figures.—(2). The left lobe of the process of the left hemitergite is smoothly elliptical, and broader than in *P. trinitatis*.—(3). The left cercus-basipodite (Anhang des 9. Sternites) is different in form, apparently having no incurved hook underlying the hypandrium (trägt aussen einen kleinen stumpfen Zapfen, innen zwei stumpfe Ecken).

I am unwilling to reduce the specific status without personal study of the types or of other material from the same region. The relationship to the species re-described below is close, perhaps closer than to *P. trinitatis*.

PARARHAGADOCHIR TRACHELIA (Navás 1915). Figs. 51–66.

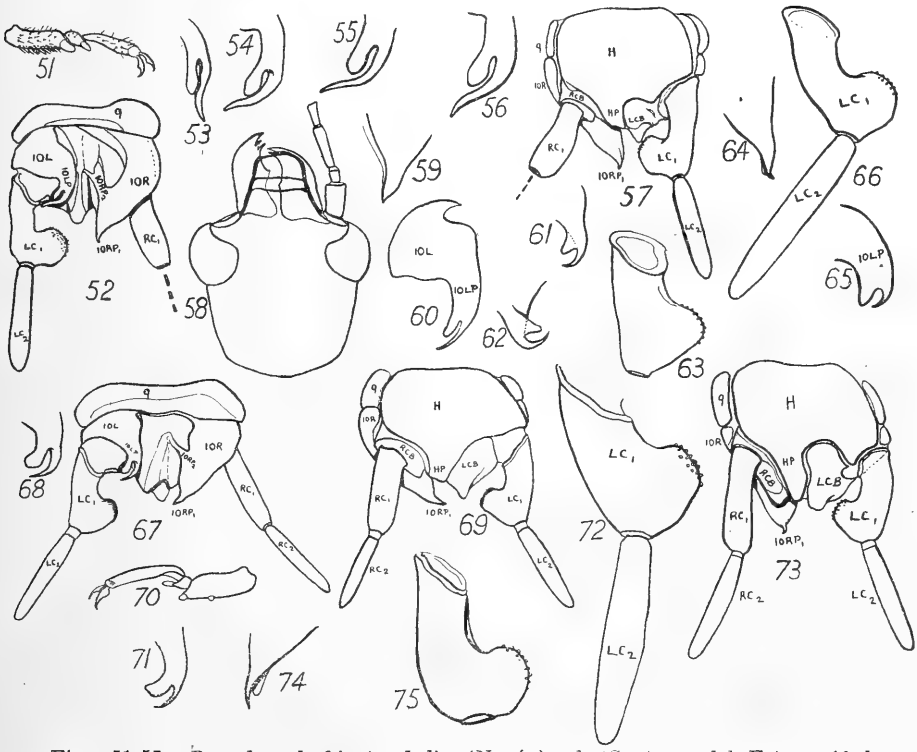
Rhagadochir trachelia Navás 1915, *Mem. R. Acad. cienc. y artes de Barcelona*, vol. 12, no. 7, p. 19, fig. 9.

The original description is from a male from Argentina (Santiago del Estero). I have not seen this type (Mus. La Plata); the present description is from a male (Mus. Paris), also from the Province of Santiago del Estero (10 km. from Lugones, railway from Rosario to Tucuman; December 1909, coll. E.-R. Wagner); it has been identified by Navás as 'Embia trachelia' (on the label below the specimen; cf. also Navás, 1923, p. 10). It agrees with the original description (as far as it goes). The fact that it was identified by the author of the species is not as conclusive as might be supposed, as the terminalia of the dry specimen had not been prepared. Unless examination of the type should later prove the contrary, the determination may be accepted.

♂. Length 8 mm.; forewing 6 mm. × 1·5 mm.; hindwing 5 mm. × 1·5 mm. General colour rather dark brown, head especially dark, eyes black; prothorax (dry) yellowish-brown; wing-veins dark brown, longitudinal bands smoky-brown (i.e. colour throughout as in *P. trinitatis*). Head, venation, and hind tarsi (Fig. 51) as in *P. trinitatis*. Terminalia (Figs. 52–57) as in *P. trinitatis*, with the following differences: Posterior process of right hemitergite ($10RP_1$) simply tapered, without any apparent membraneous lobe; process of left hemitergite (10LP) with left-hand lobe broadly elliptical, right-hand lobe longer, somewhat sinuous; first segment of left cercus (LC_1) with inner echinulate lobe not directed at all forward; and left cercus-basipodite (LCB) obtusely tapered, without an incurved hook.

Also in the Paris Museum are seven males agreeing superficially with the above; time did not permit of the detailed examination of the terminalia, so that the identification is provisional. All have been identified by Navás as 'Embia trachelia'. The localities are: Two more from the same locality as above; one from (apparently) the same locality, with the further specification 'Chuna Pampa'; and one from each of the following: 'Chaco de Santiago del Estero, Bords du Rio Salado, env. d'Icaño, Jan. 1910, E. Le Moult'; 'Chaco de Santiago del Estero, Bords du Rio Salado, La Palisa del Bracho, 25 km. N.O. (N.W.) d'Icaño, Jan. 1907, E.-R. Wagner'; 'Gran Chaco, Colonia Florencia, Bords du Rio Tapenaga, 1903, E.-R. Wagner'; and 'Chaco de Santa Fé, Bords du Rio Las Garzas, 20 km. O. (W.) d'Ocampo, E.-R. Wagner, 1903'.

A series of males in the Museum of Comparative Zoology, Harvard University, from Villarrica, Paraguay (coll. F. Schade), appears to be referable to *P. trachelia* (Nav.). Two of these were examined in detail:



Figs. 51-57.—*Pararhagadochir trachelia* (Navás), ♂ (Santiago del Estero, 10 km. from Lugones; Mus. Paris). 51. Hind tarsus viewed laterally, × 23. 52. Terminalia from above, × 23. 53-56. Process of left hemitergite, various aspects, × 50. 57. Terminalia from below, × 23.

Figs. 58-63.—*Pararhagadochir trachelia* (Navás), ♂ (Villarrica, Paraguay; Museum of Comparative Zoology). 58. Head from above, × 25. 59. Posterior part of right hemitergite, viewed from above, × 50. 60. Left hemitergite viewed from above, × 50. 61. Process of left hemitergite viewed from above, and slightly to the right and in front, × 50. 62. The same viewed from below and behind, × 50. 63. First segment of left cercus from above, × 50.

Figs. 64-66.—*Pararhagadochir trachelia* (Navás), ♂ (Villarrica, Paraguay; Museum of Comparative Zoology. Second specimen referred to in text). 64. Posterior process of right hemitergite from above, × 50. 65. Process of left hemitergite from above and to the right, × 50. 66. Left cercus from above, × 50.

Figs. 67-69.—*Pararhagadochir argentina* (Navás), ♂ (Las Garzas; Mus. Paris), 67. Terminalia from above, × 23. 68. Process of left hemitergite viewed from above and to the right, × 50. 69. Terminalia from below, × 23.

Figs. 70-73.—*Pararhagadochir argentina* (Navás), ♂ (Villarrica, Paraguay; Museum of Comparative Zoology). 70. Hind tarsus viewed laterally, × 50. 71. Process of left hemitergite from above, × 50. 72. Left cercus from above, × 50. 73. Terminalia from below, × 25.

Figs. 74-75.—*Pararhagadochir argentina* (Navás), ♂ (Villarrica, Paraguay; Museum of Comparative Zoology. Second specimen referred to in text). 74. Posterior part of right hemitergite viewed from above and to the right, × 50. 75. First segment of left cercus from above, × 50.

(1) (Collected in January; Figs. 58–63): Length 6·4 mm.; head 1·2 mm. × 0·9 mm.; forewing 5·6 mm. × 1·4 mm.; hindwing 5·2 mm. × 1·5 mm. Colour, head (Fig. 58), venation and hind tarsi as in the specimen described above; terminalia (Figs. 59–63) also substantially in agreement, but with slight differences in the process of the left hemitergite and the left cercus.

(2) (Collected in December; Figs. 64–66): Length 7·0 mm.; head 1·2 mm. × 0·9 mm.; forewing 5·4 mm. × 1·4 mm.; hindwing 5·0 mm. × 1·5 mm. Colour, head, hind tarsi, and terminalia agreeing with the above, but with slight variations in the posterior process of the right hemitergite (Fig. 64; trace of an inner membraneous lobe apparent), the process of the left hemitergite (Fig. 65; lobes of process shorter), and the first segment of the left cercus (Fig. 66; echinulate lobe somewhat different in form).

PARARHAGADOCHIR ARGENTINA (Navás 1918). Figs. 67–75.

Embia (*Rhagadochir*) *argentina* Navás 1918, *Brotéria*, Série Zoológica, vol. xvi, p. 104, fig. 4.

This species was described from two males from Argentina, one from Punta Lara, Province of Buenos Aires, coll. C. Bruch, 13/10/15 (Mus. La Plata), the second from Santa Fé, coll. P. Muhn, 6/1/15 (Navás Collection). The first-named may be regarded as the holotype. A full description of this specimen would be very desirable.

Two males in the Paris Museum (Chaco de Santa Fé: Las Garzas, Bords du Rio Las Garzas, 25 kil. O. (W.) d'Ocampo, E. R. Wagner, 1903) have been identified by Navás as 'Embia argentina' (on the labels below the specimens; cf. also Navás, 1923, p. 10). The terminalia of these dried specimens had not been prepared, so that the identification by Navás, the author of the species, again cannot be taken as positive. The following description and figures (67–69) are from one of these males.

♂. Length 8·5 mm.; forewing 6·5 mm. × 1·5 mm.; hindwing 5·5 mm. × 1·5 mm. Colour as in *P. trachelia* (Nav.), but with the prothorax concolorous with the rest of the body. Head as in *P. trachelia*, but with the hind part a little squarer. Venation as throughout the genus. My notes on the hind tarsus of this specimen are inconclusive, but it would appear from other specimens (infra) that this series has two metatarsal bladders, in contradistinction to other members of the genus studied. Terminalia (Figs. 67–69) within the range of *P. trachelia* (Nav.) as recognized above.

A series of males in the Museum of Comparative Zoology, Harvard University (Villarrica, Paraguay, coll. F. Schade) appears to be referable to *P. argentina* (Nav.). Two of these were studied in detail:

(1) (Collected in August; Figs. 70–73): Length 8·5 mm.; head 1·4 mm. × 1·0 mm.; forewing 5·9 mm. × 1·4 mm.; hindwing 5·4 mm. × 1·6 mm. Colour as in the Las Garzas specimen, i.e. prothorax concolorous. Head and venation as in Las Garzas specimen. Hind tarsi (Fig. 70) with two definite ventral bladders on first segment. Terminalia (Figs. 71–73) essentially as in the Las Garzas specimen.

(2) (Collected in November; Figs. 74–75): Length 8·5 mm.; head 1·5 mm. × 1·0 mm.; forewing 6·0 mm. × 1·5 mm.; hindwing 5·5 mm. × 1·5 mm. Colour, head, venation, and hind tarsus as in the preceding specimen. Terminalia as in the preceding, with minor differences, e.g. the posterior process of the right hemitergite (Fig. 74) has an extra membraneous lobe, and the echinulate lobe of the first segment of the left cercus (Fig. 75) is directed slightly forward.

Finally, I have received details from Mr. E. S. Ross, of the University of California, of a male from Sierra Córdoba, Argentina (Cornell Univ. Collection). This agrees in size and colour, and in the structure of the hind tarsi and terminalia, with the present concept of *P. argentina*.

Note.—The last word concerning *Pararhagadochir trachelia* and *P. argentina* will depend on a thorough examination of the types (Mus. La Plata); supplementary data could be obtained by a detailed examination of those series in the Museum of Comparative Zoology and the Paris Museum, some specimens of which have been described above. On the present data, *P. argentina* seems to differ from *P. trachelia* in the more robust build, squarer shape of the hind part of the head, concolorous prothorax, additional hind metatarsal bladder, and possibly in its earlier appearance in the season. The intra-specific variability observed in the present concepts of the two species, i.e. minor details in the terminalia, should be noted in weighing specific or subspecific criteria in this genus. The variation in the posterior process of the right hemitergite ($10RP_1$) is probably unimportant; the appearance of an additional membraneous lobe, noted in some specimens of each of these species, may well depend on chance occurrences in preservation and preparation. The variations in other structures (e.g. the left hemitergite and cercus, and the cercus-basipodites) seem more likely to represent original structural differences.

Little emphasis can be attributed to the fact that the figures given by Navás (1918, figs. 4*a*, 4*b*), for parts of the terminalia of *P. argentina*, fail to agree with the present description of this species.

PARARHAGADOCHIR sp. indet. Figs. 76–79.

A single male in the Museum of Comparative Zoology (Parintins, Brazil, 2/x/–, coll. Parish) does not appear to be referable to any known species, but it seems unwise to erect a new species, in such a difficult genus, on a single specimen. Full details are given, as several interesting characters are present:

♂. Length 5 mm.; head 1·1 mm. × 0·9 mm.; forewing 3·6 mm. × 1·2 mm.; hindwing 3·4 mm. × 1·2 mm. General colour dark brown, prothorax concolorous. The form of the head (Fig. 76) agrees with *P. trinitatis*. The hind tarsi (Fig. 77) have but one bladder present on the ventral surface of the first segment, and this is placed distally; but in a mid-ventral position on this segment, i.e. in the position where an extra bladder occurs in *P. argentina*, as well as in members of many other genera, there is an area, free from setae, where the pigmentation and sclerotization are weak, though no protuberance of this area occurs. The terminalia (Figs. 78–79) are suggestive of *P. trinitatis* in some respects, with the following differences: The base of the process of the left hemitergite (10LP) is broader; the echinulate lobe of the first segment of the left cercus (LC_1) is very smoothly rounded; the left cercus-basipodite (LCB) is obtusely tapered, without an incurved hook, thus agreeing with *P. trachelia* and *P. argentina*, in opposition to *P. trinitatis*; and the right cercus-basipodite (RCB) is slightly different in form.

In some respects, this specimen agrees more closely with *P. tenuis* (End.) and *P. adspersa* (End.) (infra) than with the species described earlier. In spite of its small size, the venation of this specimen is no weaker than in other members of the genus.

I have received from Mr. E. S. Ross details of a specimen (♂) which appears to agree with the above in most respects. This specimen is from Saramacca, Surinam (Cornell Univ. Collection).

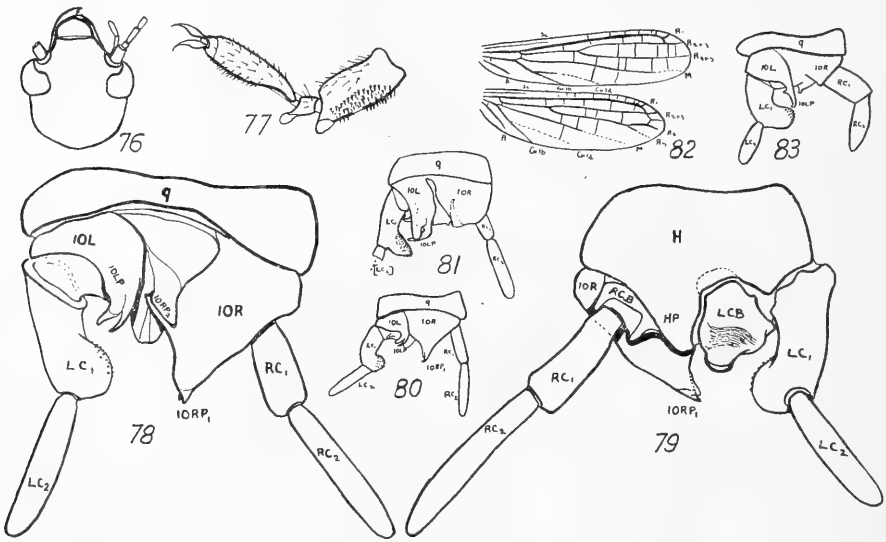
PARARHAGADOCHIR TENUIS (Enderlein 1909). Fig. 80.

Embia tenuis Enderlein 1909, *Zool. Anz.*, Bd. 35, p. 186.—*Rhagadochir tenuis* Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 60, figs. 34–35.

♂ (after Enderlein, 1909, 1912): Length 6·5 mm. (approx.); length of forewing 6 mm., of hindwing 5¼ mm. (approx.). General colour dark brown, eyes black; wings pale brown with hyaline lines, veins brown. Head and wings as in *P. flavicollis*; number of tarsal bladders not stated. Terminalia as in Figure 80 (after Enderlein, 1912, fig. 34).

Locality.—Bolivia: Provinces of Sara and Yungas. Types in Stettin and Berlin Museums.

The terminalia do not differ greatly from *P. argentina*, which this species would displace if the synonymy were proved. Without first-hand study of the types, the relationship cannot be gauged.



Figs. 76-79.—*Pararhagadochir* sp. indet., ♂ (Parintins, Brazil; Museum of Comparative Zoology). 76. Head from above, × 17. 77. Hind tarsus viewed laterally, × 47. 78. Terminalia from above, × 50. 79. Terminalia from below, × 50.

Fig. 80.—*Pararhagadochir tenuis* (Enderlein), ♂. Terminalia from above, × 16. (After Enderlein, 1912, fig. 34.)

Fig. 81.—*Pararhagadochir adspersa* (Enderlein), ♂. Terminalia from above, × 12. (After Enderlein, 1912, fig. 32.)

Figs. 82-83.—*Calamoclostes albistriolatus* Enderlein, ♂. 82. Right fore- and hindwings, × 3. 83. Terminalia from above, × 10. (After Enderlein, 1912, figs. 10, 11.)

PARARHAGADOCHIR ADSPERSA (Enderlein 1909). Fig. 81.

Embia adspersa Enderlein 1909, *Zool. Anz.*, Bd. 35, p. 185.—*Rhagadochir adspersa* Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 58, figs. 32–33.

♂ (after Enderlein, 1909, 1912): Length 9 mm.; length of forewing 10·5 mm., of hindwing 9·5 mm. General colour as in the preceding species, wings very finely flecked with brown; structure of head, and venation, as throughout the genus. Number of hind metatarsal bladders not stated. Terminalia as in Figure 81 (after Enderlein, 1912, fig. 32).

Locality.—Bolivia: Province of Sara. Type in the Stettin Museum.

The broad process of the left hemitergite, and the relatively long internal lobe of the first segment of the left cercus, appear to differentiate this species clearly from any other named species.

Note.—The genus *Pararhagadochir* offers considerable difficulty both in its relationship to other genera and in the differentiation of its component species. The former may be attributed to convergence; the latter to individual variation, and also in part to the inadequacy of some existing descriptions. I have not attempted a specific key; the six previously-described species have been allowed as distinct, and details of the structure of an unnamed species have been put on record. I have adopted a conservative attitude with regard to any changes in specific status, or to the addition of new species, as I have seen material of only three of the six species, and in the case of only one, the genotype, has this been a properly-authenticated type.

Genus Calamoclostes Enderlein 1909.

Zool. Anz., Bd. 35, p. 188. Genotype, *Calamoclostes albistriolatus* Enderlein 1909, l.c., p. 189.

Neotropical Embioptera, the males winged, with R_{4+5} simple in the forewing, shortly forked in the hind; tenth abdominal tergite completely cleft, process of left hemitergite with a short lateral lobe; first segment of left cercus clavate, echinulate.

The genus may be allowed in Enderlein's sense, with a protest against the erection of a genus on a venational character present in one pair of wings of a unique specimen, in an Order in which venational anomalies are frequent: e.g. *Clothoda urichi* (Sauss.) has R_{4+5} normally forked, exceptionally simple in one or more wings.

The genus could probably be substantiated on other characters, as the terminalia of the genotype seem to differ clearly from any other known series; such a course would retain the genus, under a new concept, even if it were proved that, in the original concept, it was based on a venational anomaly.

However, having only Enderlein's line figures before me, and no details of the hind metatarsal bladders, it is impossible to place the genus, under a new concept, in the general scheme. I have therefore retained it, provisionally and temporarily, in Enderlein's sense.

Calamoclostes albistriolatus Enderlein 1909, l.c. Figs. 82–83.

♂ (after Enderlein, 1909, 1912): Length 10 mm.; length of forewing 9 mm., of hindwing 8 mm. General colour blackish-brown; wings brown, with fine hyaline inter-venal lines and hyaline striae at cross-veins. Veins dark brown. Head with rather small eyes; sides behind eyes converging posteriorly, almost straight. Number of hind metatarsal bladders not stated. Wings (Fig. 82) (in unique specimen) with R_{4+5} simple in forewing, forked in hind; M and Cu_{1a} simple, the latter subobsolescent. Cross-veins rather numerous. Terminalia (Fig. 83) with tenth abdominal tergite completely cleft; processes of right hemitergite obscure in the figure, not described; process of left hemitergite elongate, terminally curved to the left, subacute, with a small projection to the left from near the base. Right cercus with two subcylindrical segments; first segment of left cercus curved inward in a rounded echinulate lobe; second segment subcylindrical. Ventral structures not figured, nor described.

Locality.—Baños, Ecuador, at 1800 metres above sea-level. Type in Stettin Museum.

Key.

The following key distinguishes, as adequately as possible, the genera of Embioptera whose males have the process of the left hemitergite complex, the first segment of the left cercus echinulate, and R_{4+5} forked in at least the hindwings. The characters are for the males; abbreviations, as used throughout this paper and explained under the text-figures, are used for the parts of the terminalia.

1. R_{4+5} simple in forewing, shortly forked in hindwing ..... *Calamoclostes* End.
   R_{4+5} forked in all wings, the fork at least as long as the stem 2
2. Mandibles huge, overlying labrum ..... *Enveja* Navás.
   Mandibles not as above 3
3. Teeth on LC_1 less than ten, very large 4
   Teeth on LC_1 smaller, less than ten in number 5
4. Hind legs with one ventral bladder on metatarsus; M tending to fork ..... *Donaconethis* End.
   Hind legs with two ventral bladders on metatarsus; M simple .. *Odontembia* Davis
5. LC_1 with more than one echinulate lobe internally; Cu three-branched ..... *Dihybocercus* End.
   LC_1 with only one internal echinulate lobe; Cu two-branched 6
6. R_{4+5} subobsolescent beyond fork ..... *Navásiella* Davis.
   R_{4+5} not as above 7
7. 10LP with a distal concavity between lobes 8
   10LP with lateral lobe very short, no distal concavity ..... *Parachirembia* Davis.
8. $10RP_2$ a flat elliptical flap, separated from 10R by membrane except at posterior limit 9
   $10RP_2$ not as above 10
9. Two large bladders on ventral surface of hind metatarsus; RCB very large ..... *Macrembia* Davis
   One hind metatarsal bladder; RCB small ..... *Chirembia* Davis.
10. Hind metatarsus with two bladders on ventral surface; African .. *Rhagadochir* End.
    Hind metatarsus with only the terminal ventral bladder present (except in one species); Neotropical ..... *Pararhagadochir* Davis.

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Notes and Corrigenda.

The following notes and corrigenda refer to Parts i–xiv of this Series of papers, published in these Proceedings, vol. lxiv, 1939.

Part i: Page 188, lines 14–15, for *O. ruficollis* de Saussure, 1896 read *O. ruficollis* (de Saussure, 1896), Krauss, 1911

Part iv: Page 374, line 5 from bottom, *for* having *read* have

Part v: Page 382, line 11, '*Dihybocercus berlandi* Navás 1922, and *D. gromieri* Navás 1934': The latter species, though obviously congeneric with the former, was described as *Embia gromieri*, and had in fact never been referred to *Dihybocercus*.

Part vi: Page 475, Explanation to Figs. 1–3, for *ferrox* read *ferox*. At bottom of page, from 'Conventional' to end, *read*

Conventional lettering for venation.

9, ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, $10RP_2$, posterior and inner processes of 10R; 10RP, process of 10R (when only one is present); LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; H, ninth abdominal sternite (hypandrium); HP, process of H.

Part xiii: Pages 567–572, for *Berlandiella* read *Berlandembia*

Part xiv: Pages 573–575, for *Saussurella* read *Saussurembia*

The two homonyms noted above are due to the fact that no reference books of names of genera were available when these papers were written. Lists of proposed new genera were sent to a friend in Sydney, from whom the erroneous information was received that none was preoccupied. My thanks are due to Mr. G. P. Whitley, of the Australian Museum, for calling the homonymy to my attention. The details are set out below.

Berlandembia, nom. nov.

Berlandiella Davis 1939, Proc. Linn. Soc. N.S.W., lxiv, 5–6, p. 567. Non *Berlandiella* Mello-Leitão 1929, *Arch. Mus. nac. Rio de Janeiro*, 31, p. 122 (Arachnida).

Saussurembia, nom. nov.

Saussurella Davis 1939, Proc. Linn. Soc. N.S.W., lxiv, 5–6, p. 573. Non *Saussurella* I. Bolivar 1887, *Ann. Soc. ent. Belgique*, 31, p. 196 (Orthoptera).

THE UPPER PALAEOZOIC ROCKS IN THE COUNTRY BETWEEN THE MANNING AND KARUAH RIVERS, NEW SOUTH WALES.

By A. H. Voisey, M.Sc.,* Lecturer in Geology and Geography at the New England University College.

(Plate v; two Text-figures.)

[Read 27th March, 1940.]

This paper deals with certain aspects of the geology of the country lying between the Manning and Karuah rivers in New South Wales. Owing to the removal of the writer to Armidale there is little possibility of completing the investigations, which were commenced in 1937; the results obtained are therefore submitted as a contribution to the geology of a most interesting region.

The accompanying sketch-map (Plate v) is not an accurate geological map of the area, but is intended to act as a locality guide and to indicate broadly the occurrences of the principal rock types. Geological mapping had not reached the stage where definite boundaries could be drawn between the different groups of rocks.

Previous Literature.

The general problem of the stratigraphy of the Carboniferous System was reviewed by S. W. Carey and W. R. Browne (1938), who discussed the Gloucester sequence in particular; C. A. Sussmilch (1921) has also dealt with the Gloucester area. Other references to the region are contained in papers by J. E. Carne (1897), W. N. Benson (1916), S. W. Carey (1934*b*) and G. D. Osborne (1937). Dr. G. D. Osborne has been engaged for some time past in collecting data relating to the Gloucester Trough and allied structures. His earlier work on the stratigraphy and structure of the area immediately to the south is well known.

Geological Structures and Rock Distribution.

The Carboniferous and Kamilaroi strata form a synclinal structure known as the Gloucester Trough which has a generally meridional trend and extends from Gloucester to the neighbourhood of Stroud. Osborne (1937, p. 387) noted that there was a remarkable swing in the strike between Booral and Stroud.

Another syncline was described by Carey (1934*b*) from the Bullah Delah District. This has a general trend N. 27° W., and, like the Gloucester Trough, consists of Carboniferous and Kamilaroi beds. He called it the Bullah Delah Syncline.

An anticlinal structure, almost certainly affected by meridional faults, is inferred between these two down-folds.

As described elsewhere (Voisey, 1939*b*), the Devonian rocks are bounded on the north by the Manning River Fault System. They appear to be faulted against the Carboniferous in places to the south, but there may be conformity between Upper Devonian and Lower Carboniferous strata in the region lying immediately to the north of the Wang Wauk River. The boundary between the two has not been defined so far and is here indicated only tentatively.

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* Work done while the writer held a Linnean Macleay Fellowship in Geology.

Devonian sediments occur also in the neighbourhood of Copeland, where, it is believed, they bear faulted relationships with the Lower Carboniferous beds.

Stratigraphy.

Kamilaroi.

The Gloucester Coal Measures.

Shales, sandstones, grits, conglomerates and coal seams, totalling upwards of 1000 feet in thickness, according to Sussmilch (1921, p. 250), occupy the central portion of the Gloucester Trough, and outcrop intermittently between Gloucester and Stroud. Dr. Osborne (verbal communication, and 1937, map facing page 390) noted the presence of basalt in the Kamilaroi sequence. *Glossopteris* and petrified wood occur abundantly throughout the beds.

While little evidence is available, it would seem that, as pointed out by Sussmilch (1921), the Gloucester Coal Measures are the equivalents of the Upper or Newcastle Coal Measures.

The basal Kamilaroi conglomerates appear to have been deposited directly upon the Gloucester Rhyolites at the top of the Carboniferous sequence. The possibility that strike faults separate the two groups of rocks cannot be eliminated without detailed examination of the contact. It can only be stated that the writer, wherever he has examined the junction on the eastern and western limbs of the syncline, observed the same general sequence from lavas to conglomerate without any evidence of faulting. Moreover, no other worker has produced evidence of the presence of major faults there.

Certain important issues arise if it is accepted that the conglomerates were deposited upon the lavas. So important are these that any further information relating to this junction should be recorded.

If the Gloucester Coal Measures are the equivalents of the Upper Coal Measures, the question arises as to what was happening in the Gloucester District during the remainder of Kamilaroi time. Either there was deposition of sediments which were removed before the Gloucester Coal Measures were laid down, or the Carboniferous beds must have formed a land surface which underwent some erosion. If the second alternative is accepted there is quite sufficient explanation for the apparent absence of the well developed glacial beds in the Upper Kuttung Series.

Bullah Delah Beds.

Osborne's map (1929, p. 457) showed Kamilaroi sediments in the neighbourhood of Bullah Delah. Carey (1934) mentioned the occurrence of Upper Marine fossils within the village, preserved in a fine-grained tuffaceous sandstone. He stated further that the Greta Coal Measures were indicated by coal outcrops in portions 119 and 67, Parish of Bullah Delah, and that *Gangamopteris* was collected from shales associated with the former outcrop. No Lower Marine beds were found by him or by the writer. It would appear that the series is overlapped by the Greta Coal Measures in this locality as it is at places in the Hunter Valley.

Carboniferous.

A. Stratigraphical Sections, etc.

Barrington Section.

C. A. Sussmilch (1921, p. 242) measured a section from Barrington–Copeland Road to the trigonometrical station on The Gloucester Buckets and then easterly across the syncline. From this he calculated a thickness of 12,410 feet of Carboniferous beds.

Another interpretation of the general sequence, based on a reconnaissance traverse by Dr. W. R. Browne and the present writer, was given by Carey and Browne (1938, p. 597). These writers limited the Upper Burindi Series to the beds between the base of the lowest lava flow and the top of the highest bed containing marine fossils. Their interpretation, apart from the question of the separation of the Carboniferous series on different grounds from those used by Sussmilch, added a lava flow between the *Productus barringtonensis* bed and the Plant beds. Carey and Browne took the view also that the Conglomerates and *Rhacopteris* beds were considerably thicker than indicated by Sussmilch. In addition, Browne identified varve shales in the sub-Gloucester Rhyolite beds of the Cut Hill section.

Carey and Browne (1938, p. 597) pointed out that the lava flow taken by them as the base of the Upper Burindi (= Lower Kuttung) Series marked a change from the compact bluish-green Burindi rock types to the light-coloured tuffs which characterize the Kuttung Series in other areas. The flow itself cannot be used safely as the marker bed since, at the present time, its continuity cannot be guaranteed. However, it was traced through a distance of about four miles by the writer. In the absence of more detailed information it serves the useful purpose of allowing an approximate division to be made between the two series.

Separation of Upper Kuttung from the Upper Burindi (= Lower Kuttung) is difficult since beds containing plant fragments occur in the marine sequence and there does not appear to be any marked lithological change. Browne and the writer, in their examination of this section, regarded some cherty beds with plants as doubtfully belonging to the Upper Kuttung (see Carey and Browne, 1938, p. 597). Following an examination of the Gap Section the present writer is now inclined to place these beds and the rhyolite above them in the Upper Burindi and to take the tuffs and their intercalated conglomerates as the basal unit of the Upper Kuttung. The implied lithological change indicated by the mention of conglomerates is not so definite as it would seem, since these form only a small fraction of the total thickness of tuff and mudstone, and are not concentrated at the base of this major unit.

McInnes's Farm Section.

The section examined by Dr. W. R. Browne and the writer runs approximately east from the Barrington–Rawdon Vale Road starting at McInnes's Farm about a quarter of a mile north of Barrington School. Road cuttings reveal rhythmically-bedded mudstones and sandy mudstones with occasional thin bands of conglomerate. Large quantities of well-preserved fossil wood, including *Lepidodendron* stems, possibly *L. Veltheimianum*, occur. Small marine gastropods and brachiopods were found in the conglomerates which are characterized by small green cherty pebbles. South of the school these beds overlie the oolitic limestone horizon. Tuffs which grade almost into breccias in places follow the plant beds and constitute what may be regarded as the topmost unit of the Lower Burindi Series.

The quartz keratophyre (No. 2 Flow of Sussmilch) then forms a low ridge. Overlying the lava are the light-coloured tuffs of the typical Kuttung type which underlie the next flow of quartz keratophyre (No. 3 Flow of Sussmilch). This is succeeded by similar tuffs and the conspicuous and important *Productus barringtonensis* bed which gives rise to a prominent ridge. The coarse tuff contains numerous specimens of the brachiopod which are exceedingly well preserved considering that the matrix is composed of large felspar and quartz

grains. The rock weathers to a brown spongy material with large cavities representing the shells of the productids which have been dissolved out. By ascending a spur east of the fossil bed one crosses a great thickness of tuffs and mudstones. Some horizons are packed with marine fossils, the following forms being collected by the writer (probably = horizon X7 of Gap Section): *Fenestella*

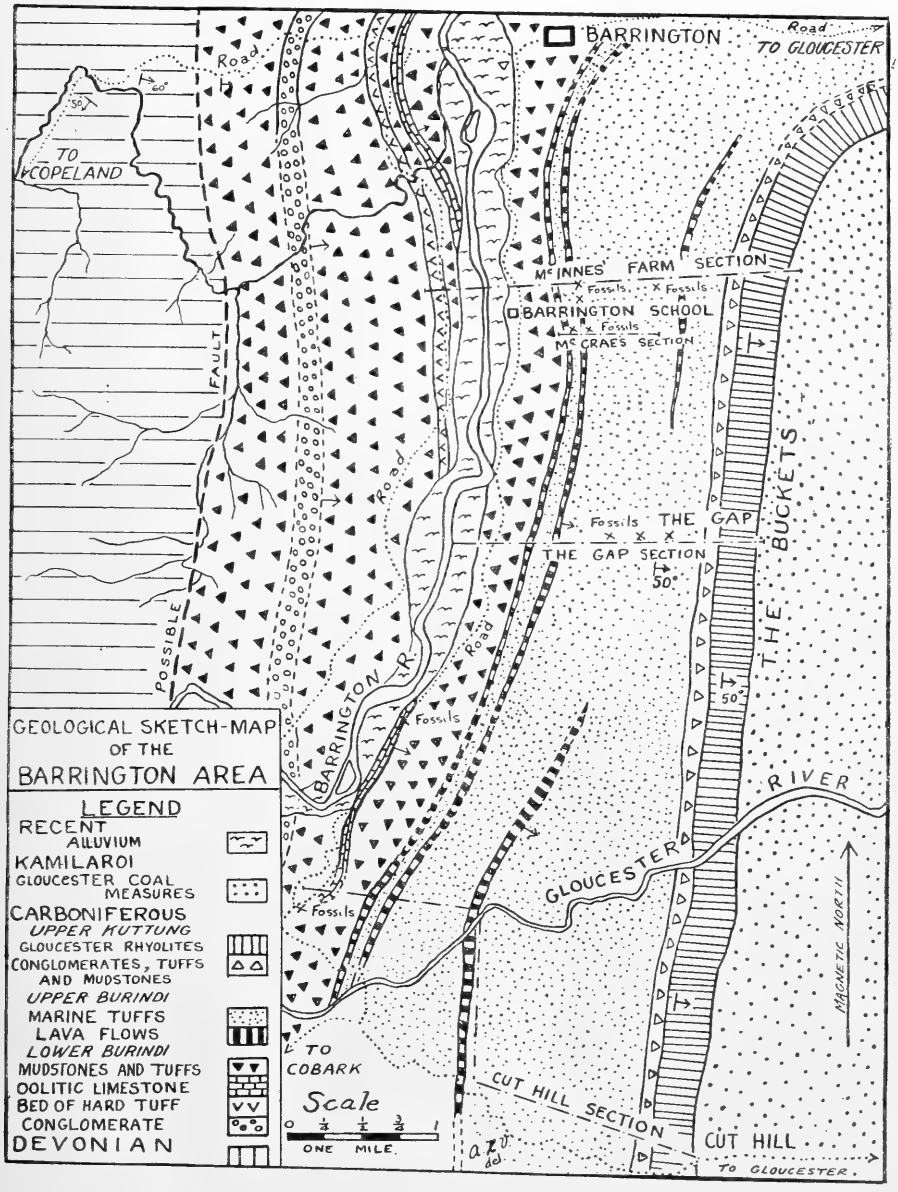

Fig. 1.

spp., abundant Crinoid stems, *Spirifer pinguis* (Sowerby), ? *Actinoconchus planosulcatus* (Phillips), *Productus pustulosus* (Phillips), *Aviculopecten flexicostatus* Mitchell, *Cordania gardneri* Mitchell, and a new genus of pelecypoda. (Specimens F38026–42, Aust. Museum Coll.)

Among these marine beds is a flow of acid lava which outcrops at the top of the main ridge. In rugged country between this and the main lava flow at the top of the Upper Kuttung sequence are tuffs, conglomerates, mudstones and cherty rocks containing plant remains. Sussmilch (1921) collected fossil plants from tuffs and shales immediately below the Gloucester Rhyolites which terminate the Upper Kuttung succession.

The section described above was not measured accurately, but the sequence is indicated in figure 2.

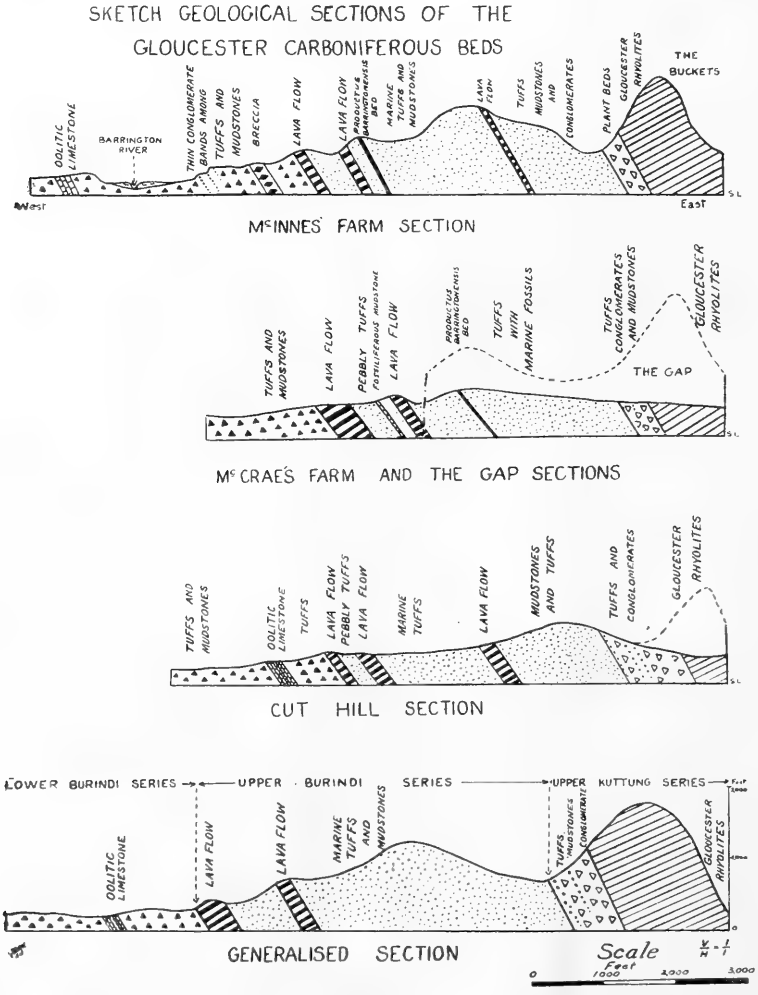

Fig. 2.

McCrae's Farm Section.

Sussmilch (1921, p. 246) mentions McCrae's Farm (Portion 4, A.A. Co.'s subdivision) as one of the places where the *Productus barringtonensis* bed outcrops. This and associated beds were traced from McInnes's Farm southward, and the following section was measured then in an easterly direction on the north side of a creek.

	Approx. Thickness. Feet.
Upper Burindi Series.	
Tuffs with marine fossils (*Productus barringtonensis* bed being included in the group)	400 plus
Lava flow (Sussmilch's No. 3 Flow)	150
Coarse, medium and fine tuffs	180
Mudstones with marine fossils (horizon W1)	10
Coarse pebbly tuffs	200
Medium textured tuffs	350
Lava flow (Sussmilch's No. 2 Flow)	400
	1,690 plus

The fossil bed, horizon W1, was found a short distance east of the ridge of lava (No. 2 Flow). The fossils contained in it include: *Productus* sp. indet., *Orthis valida* Dun, ? *Actinoconchus planosulcatus* Phillips sp., *Chonetes* sp., *Productus semireticulatus* Martin sp., *Strophomena analoga* Phillips.

The Gap Section.

A section was measured across the Upper Carboniferous strata between a point on the road on the east side of Barrington River, a mile and a half south of Barrington Public School (in the neighbourhood of portion 62, parish of Verulam) and the Gap. The traverse was made close to the present boundary fence between the properties of Messrs. H. C. Perram and G. A. Wesley.

	Approx. Thickness. Feet.
Upper Kuttung.	
The Gloucester Rhyolites	1,000 plus
Tuffs, conglomerates and mudstones	350
Upper Burindi.	
Tuffs and dark grey mudstones	500
Medium to coarse grained tuffs	50
Tuffs with abundant marine fossils (horizon X7)	300
Coarse tuffs with bands of marine fossils (horizon X6)	40
Fine-grained tuffs and mudstones (horizon X5)	140
Coarse tuffs with marine fossils (horizon X4)	80
Coarse tuffs	120
Fine-grained tuffs	70
Coarse tuffs with rounded pebbles in some bands	120
Limestone and tuff (horizon X3)	10
Coarse tuffs	450
Fine-grained tuffs with marine fossils (horizon X2)	15
Productus barringtonensis bed of coarse tuff (horizon X1)	30
Tuffs	300
Lava flow (No. 3 flow)	250
Tuffs and mudstones	200
Lava flow (No. 2 flow)	150
	4,175 plus

The outcrops of the four last-mentioned units were poor, so that the thicknesses given are not reliable. Details of this part of the sequence may be ascertained from adjacent sections, notably that of McCrae's Farm.

The *Productus barringtonensis* bed and overlying marine tuffs and mudstones here form a saddle between two much higher ridges which are partly composed of these units. The tuffs and mudstones which follow them also contain a well developed marine fauna. Collecting was done from a number of beds and the fossils are distributed as follows:

Horizon X7.—*Productus pustulosus* Phillips (abundant), *Spirifer* cf. *pinguis* Sowerby, ? *Actinoconchus planosulcatus* Phillips.

Horizon X6.—Indeterminate pelecypod, indeterminate cast of *Spirifer*.

Horizon X5.—Indeterminate brachiopod fragments, internal cast of gastropod, internal cast of *Spirifer*.

Horizon X4.—Indeterminate specimens.

Horizon X3.—*Chonetes* sp. indet.; possibly 2 species present, viz.: *Chonetes papilionacea* and *C. hardrensis*.

Horizon X2.—*Camarotoechia* cf. *pleurodon* Phillips, *Spirifer* indet. sp.

Horizon X1.—*Productus barringtonensis* Dun, *Productus* sp. indet., indeterminate pelecypod.

The tuffs vary considerably in texture, grading from mudstones into gritty rocks with large rounded pebbles in them. They are mostly, if not all, water-sorted, and in some cases could be called ordinary grits and sandstones. However, most of the beds are tuffaceous. The great number of shells present in horizon X3 has given rise to a rock which is almost wholly composed of calcium carbonate.

Above the prolific fossil horizon, Zone X7, there appears to be little change in the nature of the tuffs. Only the tuffs outcrop in the paddocks, but the creek which flows through the Gap exposes dark grey mudstones which dip generally east at 50 degrees. It is apparent that the mudstones are far more abundant in the sequence than outcrops indicate, since they are only exposed by creeks or cuttings. Their presence must be inferred among the tuffs which are listed in the section given. The section taken across Cut Hill contains more mention of the mudstones, since observations were made of the rocks in road cuttings.

Several thin bands of conglomerate consisting of well-rounded lava pebbles occur in some of the more massive tuff beds and grade into them. As in the Cut Hill sections, these units are of minor importance and do not differ greatly from the tuffs lower in the sequence which contain similar pebbles scattered more sporadically. Separation of the conglomerates and associated tuffs from the underlying beds would be arbitrary and not justified by field evidence. That some change in the nature of the sedimentation must have occurred somewhere in the sequence is indicated by the evidence supplied by Sussmilch that plant beds occur between the conglomerates and the Gloucester Rhyolites. No trace of such plant beds was found on the traverse taken—deposits of Recent breccias of rhyolite covering the rocks immediately below the lavas. Any plant beds which might be present are grouped in the thickness of 350 feet as tuffs, conglomerates and mudstones.

Cut Hill Section.

A section was measured from the Barrington–Rawdon Vale Road east through portions 117 and 86, parish of Verulam, to the Gloucester River. There an offset was made to the south and the section was continued over Cut Hill along the

Gloucester–Rawdon Vale Road to the ridge of rhyolite at the top of the Upper Kuttung sequence. The whole section corresponds with those measured near Barrington and McInnes's Farm several miles to the north.

The succession of beds in descending order is as follows:

	Approx. Thickness. Feet.
Upper Kuttung.	
The Gloucester Rhyolites	500 plus
Tuffs and mudstones (plant beds?)	500
Tuffaceous conglomerate	30
Tuffs	25
Tuffaceous conglomerate	40
Tuffs with subordinate mudstone	170
Tuffaceous conglomerate	10
Upper Burindi.	
Mudstones and subordinate tuffs	430
Tuffs	90
Tuffs and mudstones	500
Mudstones with bands of tuff	60
Greenish-grey mudstones	175
Acid lava	225
Fine-grained tuffs with cherts containing fragmental plant remains	120
Coarse tuff with marine fossils	110
Fine-grained light grey tuffs	60
Light grey tuffs with conglomerate bands	110
Gritty tuffs	100
Massive coarse tuffs with lava pebbles	60
Grey tuffs with plant remains	440
Gritty tuffs	80
Acid lava (No. 3 flow)	250
Pebbly tuffs and medium-grained tuffs	280
Acid lava (No. 2 flow)	100
Lower Burindi.	
Fine-grained tuffs with fragmental plant remains	80
Coarse tuff with well-rounded pebbles	80
Coarse felspathic tuff (marine fossils)	75
Tuffs	110
Light-coloured tuffs	40
Mudstones and tuffs (marine fossils, horizon V1)	10 plus
Fine-grained light-coloured tuffs	150
Oolitic limestone	20
Mudstones with marine fossils (horizon U1)	75
Oolitic limestone	30
Banded mudstones	5
Tuffs with conglomerate bands	50
	5,190 plus

Addition of the beds below horizon V1 was carried out with reference to a section measured about a mile north of the main traverse, approximately in portion 55, parish of Verulam.

The composite section commences with greenish-grey tuffs which are separated by thin bands of conglomerate containing small green pebbles. The beds are exposed by cuttings on the Barrington–Rawdon Vale road. They are overlain by banded mudstones and the oolitic limestones. Thinly-bedded greenish-grey mudstone with some sandy phases separates the two limestone horizons and contains the following marine fossils (horizon U1): *Chonetes aspinosa* Dun (F38755–8), *Spirifer striata* Sowerby, *Productus* cf. *pustulosus* Phillips, *Productus semireticulatus* Martin, *Spirifer pinguis* Sowerby.

The limestones contain similar fossils, not so well preserved. The green pebbles so characteristic of the conglomerate bands also occur in the calcareous rock.

Fine-grained light-coloured tuffs follow and pass into gritty tuffs. Within this unit mudstone bands containing marine fossils occur. From a road cutting on the east of the Barrington–Rawdon Vale road in the southern part of portion 117, Parish of Verulam, the following fossils were obtained (horizon V1): "*Leptaena analoga*" Phillips, *Productus* sp., *Spirifer pinguis* Sowerby, *Spirifer striata* Sowerby.

Fragments of marine fossil shells occur throughout the next few hundred feet of coarse tuffs and tuffaceous conglomerates. Plant remains occur in the tuffs below the first lava flow in the sequence. These beds closely resemble those above the lava and are unlike the Lower Burindi types. However, on the arbitrary basis of subdivision adopted for the time being, they must be retained in the lower series (because they underlie the lowest lava flow).

Following these tuffs is the Upper Burindi Series which contains coarser tuffs, passing into conglomerates in places. They are interbedded with flows of acid lava. Traces of plants and marine shells are abundant, but no well preserved fossils were found on this traverse, hence the positions of the beds in relation to the fossil zones are doubtful.

Finer grained tuffs and mudstones were met higher in the sequence.

The reappearance of conglomerate bands, much coarser than those lower down, has been taken to indicate the basal stage of the Upper Kuttung Series. Thereafter, except for a more or less well defined conglomerate band, the strata consist of tuffs and fine-grained mudstones, some of which are probably glacial in origin. The glacial rocks or varve-shales were first recognized by Browne (Carey and Browne, 1938, p. 598). The conglomerates are made up of rounded pebbles of the hard rock types set in a tuffaceous matrix. They are almost certainly the result of water-sorting and not of glacial influences. The coarse rocks are well distributed through the sequence in this section and are subordinate to the finer-grained sediments. They do not form a well defined basal unit.

At least 500 feet of acid lavas known as the Gloucester Rhyolites terminate the Carboniferous section. The variation in the thickness of this unit from point to point might be due to several factors, one of which could have been erosion during early Kamilaroi times.

Nowendoc Road Section.

The McInnes's Farm and Cut Hill Sections were taken on the eastern side of the Barrington River and included only a small portion of the Lower Burindi Series. The latter, however, are well represented between Barrington and Copeland, probably being cut off by a fault on the west before giving way to Devonian beds.

The series contains a large proportion of the olive-green mudstones so typical of the Lower Burindi suites elsewhere. Hard bands of a medium to coarse tuffaceous rock separate the finer-grained crumbling sediments. One such band may be followed south for some miles on the western side of the Barrington River. It underlies the oolitic limestones and overlies similar tuffs whose outcrops may be seen running parallel to it on the western side. Outcrops of the mudstone are not good, but the Nowendoc Road exposes a fairly continuous sequence of beds commencing about half a mile from its junction with the Barrington–Copeland Road.

The following section was measured (in descending order):

	Approx. Thickness. Feet.
Olive-green mudstones	10
Grey tuffs with scattered pebbles	5
Conglomerate	20
Olive-green mudstones	40
Crinoidal limestone with mudstone bands	55
Olive-green mudstones	50
Crinoidal limestone	20
Olive-green mudstones	50
Tuffs	30
Conglomerate	15
Tuffs	10
Olive-green mudstones	30
Conglomerate	5
Olive-green mudstones	10
Conglomerate	5
Olive-green mudstones and tuffs	15
Tuffs	10
Olive-green mudstones and tuffs	40
Olive-green mudstones	10
Tuffs	40
Olive-green mudstones	10
Olive-green mudstones and tuffs	500
	980

This section is terminated by a fault which crosses the Nowendoc Road near the southern end of portion 57, Parish of Fitzroy. Devonian sediments are exposed by the road cuttings on the ridge between portions 71 and 77. Conglomerates on the road from Barrington to Copeland on a hill between portions 83 and 46 may belong to one of the beds mentioned in the above section. If this is so, some hundreds of feet of tuff lie below the conglomerates and these give way to Devonian rocks somewhere in portion 32, Parish of Fitzroy.

The nature of the junction between the Carboniferous and Devonian rocks has not been determined beyond doubt by any worker. Outcrops are discontinuous and the tuffs of the two systems, which give rise to the principal outcrops, are somewhat similar. The marked break in slope parallel to the strike of the Carboniferous rocks may be significant. Sussmilch (1921, pp. 248–249) discussed the problem, pointing out that the boundary marked on the map was approximate only. He remarked on the differences between the strikes of the two formations and on the fact that the axis of the synclinal structure containing Carboniferous and Kamilaroi rocks was opposed to the Devonian lines of folding. He suggested that these points were indirect evidence of an unconformity. Osborne (verbal communication) is of the opinion, however, that the whole sequence is conformable.

The present writer is in favour of faulting as an explanation of the discordance in strike. So many other important faults occur in this region that a major fault of this character and in this position would accord with the general fault pattern.

From the stratigraphical viewpoint it would appear that the Barraba Series of the Tamworth District is worthy of better representation than that attributed to it by Sussmilch (1921, p. 241) i.e. the beds between the six- and seven-mile posts on the Gloucester–Copeland Road. These rocks could belong to the Tamworth Series. If this is the case, either the Barraba Series has not been

developed in the area, or, as appears to be more likely, it has been faulted out of the sequence, together with some of the Lower Burindi beds. Even if the estimated thickness of 6,500 feet (Sussmilch, 1921, p. 242) is correct, and this appears to be the case, the Lower Burindi Series seems to lack certain important units. It is admitted that changes in facies might account for the differences between this section and those in neighbouring districts, such as that at O'Sullivan's Gap where a high range is composed of hard Lower Burindi strata, and that at Firefly Creek where the crinoidal limestone is prominent. Nevertheless, the writer is impressed by the apparent inadequacy of the Gloucester section and considers that the evidence, such as it is, favours a faulted junction.

Firefly Creek and Brushy Mountain.

Sussmilch (1921, pp. 243, 244) described a coarse crinoidal limestone which outcrops on the Nowendoc road. He noted that a similar limestone outcropped on the stock reserve two miles out of Gloucester and again in Tugrabakh Creek, near Brushy Mountain. The limestone on the Nowendoc Road is included in the measured section described above. The strata associated with it do not appear to correspond with those adjacent to the Brushy Mountain belt. These latter are more allied to Devonian rock-types as were those interbedded with the limestone at the quarry near Tugrabakh Creek on the Bundook road (Sussmilch, 1921, p. 240). Indeed, it would appear as if the course of Tugrabakh Creek has been determined by the presence of the limestone and its associates and that the same band runs from the Bundook road to Brushy Mountain and beyond.

Following examination of the beds mentioned above, the writer considered the Tugrabakh Creek limestone (Zone T) to be Devonian; a number of fossils collected from the neighbourhood were submitted to Dr. Dorothy Hill of the University of Queensland and Mr. H. O. Fletcher of the Australian Museum. Dr. Hill identified the following corals: *Syringopora* ? or *Cladochonus* ?; Zaphrentoid coral; *Amygdalophyllum* sp.; and *Michelinia* sp.

She suggested that the horizon might be the equivalent of the lowest of the Carboniferous limestones in the Rockhampton District of Queensland. She added that, because no columellate corals (e.g. *Amygdalophyllum*) are known from the top of the Devonian in Germany where the facies is suitable, it is reasonable to assume that the limestone is Lower Carboniferous.

Mr. Fletcher recognized *Cordania gardneri* Mitchell among crinoid stems and indeterminate gastropod remains in mudstones associated with the same limestone in the Firefly Creek area. Hence, he regards the beds as being Lower Burindi.

The Tugrabakh Creek limestone swings southward a little to the east of Brushy Mountain and can be followed from the hills to the north of the junction of Firefly Creek road and the Pacific Highway to a point where it crosses the Firefly Creek road three and a half miles from the junction. In this region it would appear as if there were two limestone horizons, but there may have been duplication by strike faulting. The strike of the bed swings round from approximately east-west to north-west–south-east.

The beds outcropping alongside the road to Bunyah include a spectacular tuffaceous conglomerate containing the remains of marine fossils. None of the fossils, which are crinoids and brachiopods, were sufficiently well preserved for identification. Associated with the conglomerate were tuffs and mudstones which could be Devonian or Lower Carboniferous in age. It is suggested, on account of the presence of the marine fossils and the variation in rock type, that the beds are Lower Carboniferous rather than Upper Devonian. However, no

unconformity or sudden lithological change was observed when the beds were crossed between Krambach and Bunyah and it would appear as if the Devonian beds pass upwards into the Carboniferous without much variation.*

Even if he accepts the correlation between the Tugrabakh Creek limestone and that on the Nowendoc Road, the writer finds it still more difficult to believe that the big thickness of beds examined in the Krambach-Bunyah district could be represented by those between Barrington and Copeland. Hence, there might here be further evidence for the alleged fault between the Carboniferous and Devonian beds in that area.

Rawdon Vale and Cobark.

Mr. Fordyce, who recently retired from the position of Shire Engineer at Gloucester, showed the writer some marine fossils of Lower Burindi age which he had obtained from the following localities: (*a*) portion 76, Parish of Barrington; (*b*) portions 44 and 31, Parish of Barrington. He stated that similar fossils were plentiful in the country about Cobark and Rawdon Vale and mentioned also fossils which were found in the neighbourhood of Berrico Mountain.

Such occurrences are of importance, particularly as some are from the west of Copeland, indicating that the outcrops of Devonian rocks are limited in a westerly direction. It would be interesting to determine whether the block so formed is entirely surrounded by faults as is the Devonian occurrence between Tinonee and Wallaby Point. The faults are believed to occur on at least three sides. (See accompanying map, Plate v.)

Booloombayt Section.

Road cuttings in a hill about four miles north of Bullah Delah towards O'Sullivan's Gap reveal very interesting Carboniferous rocks. The strata strike from northerly to north-westerly and have a very steep dip which is generally westwards or vertical. Since the beds lie on the eastern limb of the Bullah Delah Syncline it is assumed that the strata are older as one goes east or north-east. If this is so, the section measured is in descending order as follows:

	Feet.
Tuffs with thin bands of micaceous rock	100
Hard black mudstones with marine fossils	220
Grey mudstones with marine fossils	240
Productus barringtonensis bed	5
Light-coloured coarse tuffs	200
Light-grey crumbling mudstone	40
Coarse dacitic tuff containing large boulders of dacitic lava	50
Dacite?	10
Conglomerate with tuffaceous matrix containing lava boulders up to 3 feet across	20
Dacite?	20
Conglomerate with tuffaceous matrix, containing large lava boulders	50
Fine grey tuff	25
Conglomerate with tuffaceous matrix	30
	1,010

The fossils identified from the beds at the top of the sequence are *Spirifer* sp. indet., *Chonetes* cf. *hardrensis* Phillips (Australian Museum Collection, Nos. F38760–74).

The *Productus barringtonensis* (Dun), (Aust. Mus. Coll., F38759) and the lavas indicate that the beds are Upper Burindi in age and this is further suggested by

* See note to map; p. 210.

the occurrence of Lower Burindi strata lower down on the eastern limb of the Bullah Delah Syncline at O'Sullivan's Gap.

The interesting occurrence of tuffs, lavas and tuffaceous conglomerates is excellently exposed and is worthy of more detailed petrological treatment than the hurried examination which was given it.

O'Sullivan's Gap Section.

Carboniferous rocks occupy most of the area between the Myall and Wang Wauk Rivers and the Lower Burindi beds are the most widespread and conspicuous. The Lower Burindi strata comprise the principal part of a high range which forms the divide between the two rivers. The beds here probably lie on the eastern limb of the Bullah Delah Syncline, and dip consistently with such a view. However, it is probable that some faulting has occurred between them and Bullah Delah, since the high dips noted would give a very great thickness to the Upper Burindi and/or Upper Kuttung beds in an unbroken sequence.

The Gloucester–Nabiac road crosses the range at O'Sullivan's Gap and road cuttings reveal the strata particularly well. The beds dip generally south-westerly at 45°–65°. The following section (in descending order) was measured by compass and pacing traverse on the southern side of the hill:

	Approx. Thickness. Feet.
Black cherty mudstone	40
Light-coloured tuff	5
Black cherty mudstone	15
Light-coloured tuffs and mudstones	12
Micaceous rock	8
Light grey mudstones	50
Black chert	3
Light grey mudstones and tuffs	12
Tuff resembling dacite	50
Tuffaceous agglomerate	40
Black chert	60
Tuffs, etc.	30
Dacite (?)	10
Tuffs and mudstones	5
Dacite (?) and agglomerate	100
Mudstones and tuffs	300
Black mudstones	200
Grey mudstones with micaceous bands	450
Hard black cherty mudstones	15
Light grey mudstones	80
Hard mudstones and soft grey mudstones	60
Micaceous rock	5
Crumbling mudstones	100
Hard black mudstones	200
Grey mudstones	30
Hard black mudstones (Gastropod horizon)	10
Micaceous rock	5
Black mudstone	60
Grey mudstone and micaceous rock	4
Black mudstone with subordinate light grey mudstones	200
Black mudstones (*Spirifer* horizon)	30
Bluish green cherty tuffs	20
Hard blue tuffs with plant fragments	10
Black cherty mudstone	20
Massive tuffs with interbedded mudstones	100 plus
Total thickness measured	2,339 feet

The above section was underlain by a big thickness of massive tuffs with subordinate interbedded mudstones. The bends in the road prevented further measurement being made satisfactorily, and exposures on the hillsides were poor.

It would appear from the presence of the acid lavas at the top of the sequence that these beds could be included in the Upper Burindi suite. Insufficient work was done to enable a satisfactory basis of division to be made in the area.

The mudstones which make up a large part of the sequence are typically those of Lower Burindi sequences at Dungog and at Hilldale. From the last-named locality Osborne (1922) records cherty mudstones, tuffs and mica-bearing rocks which correspond closely to those in the O'Sullivan's Gap section. The micaceous rocks are also found at Kolodong near Taree in the Lower Burindi Series (Voisey, 1938).

Perhaps the most conspicuous feature of the sequence is the rhythmical bedding of the mudstones. The rocks vary slightly in their characteristics and somewhat different adjectives have been used to describe the fine-grained sediments. The mudstones range in colour from light grey to black, and frequently have a greenish tinge. They possess different textures from bed to bed and also differ in hardness. Some are almost cherts.

The tuffs are generally fine-grained and occur in beds several feet in thickness, being thicker and more massive lower down in the sequence than in the portion measured.

The rock which has been termed a dacite has not been examined petrologically since the study of the volcanic rocks of this and the Booloombayt section is deserving of detailed treatment. It is hoped that a petrologist will undertake this work and that an attempt will be made to correlate the lavas with those in the Clarencetown-Paterson District.

The Spirifer horizon contains the following fossils: *Spirifer pinguis* Sowerby, *Spirifer striata* Sowerby, Crinoid stems, *Chonetes* cf. *hardrensis* Phillips, "*Leptaena analoga*" Phillips, *Fenestella* sp., *Productus* sp.

Mograni Section.

Between Mograni Creek and Mograni Mountain good exposures of Carboniferous rocks were examined. Crinoid stems and abundant but fragmental marine fossils were found.

The section measured (in descending order) was taken about a mile and a half east of the junction of the Mograni Road and the Pacific Highway.

	Approx. Thickness. Feet.
Acid lava	80
Soft grey mudstones	110
Grey chert	40
Cherts and mudstones	30
Felsite	60
Soft mudstone	60
Banded rhyolite	110
Mudstone	200
Felsite	5
Mudstone	40
Acid lava	200
Coarse tuffs	160
Banded rhyolite with botryoidal structures	150
Coarse tuffs	200
Dark blue coarse tuffs	500
Gritty tuffs with marine fossils	50
Mudstones and tuffs	(not determined)
Total measured thickness	1,995 plus

Sussmilch (1921, Plate xviii) placed a probable fault between the sediments measured and the main volcanic beds of Mograni Mountain, evidently having noted the discordant dips of the strata mentioned above. These dips are principally vertical or to the north, and overturning is indicated.

The fault which he indicates near Mograni Cutting has been confirmed and extended further to the east and to the west.

The exact position of the sequence in the Carboniferous succession has not been worked out.

Wauk Ivory.

On the eastern side of the Gloucester Trough, Carboniferous beds outcrop in fairly rugged country north and south of the Wauk Ivory road. No sections were measured here, but a reconnaissance trip revealed essentially the same sequence as on the western limb.

Marine fossils were found in loose material beside the Wauk Ivory road by the writer, but Mr. Fordyce reported marine fossils *in situ* on portions 211 and 216 of the A.A. Company's Subdivision close to the same road.

Lower Burindi rocks appear to continue for some distance to the south-east beside the track to Upper Myall. The route is just trafficable for a motor vehicle with a high clearance, and rock outcrops for the most part are poor. Most of the sediments seen consisted of tuffs and mudstones. Some of the latter were olive-green in colour and contained bands of intraformational breccias. Near the eastern boundary of the A.A. Company's land the strikes were nearly east and west.

About 23 miles from Gloucester carbonaceous shales and impure coal seams were found associated with light-coloured tuffs. They suggested either an Upper Kuttung or Kamilaroi age for the occurrence. Five miles further on, towards Upper Myall, hills containing a spectacular tuffaceous conglomerate were observed lying to the south of the road. It is believed that these represent outcrops of Wallarobba Conglomerate, but no confirmatory mapping was done.

The road was then followed through the centre of the Bullah Delah Syncline to the village of Bullah Delah.

Myall Lakes.

Carey (1934*b*) examined the Carboniferous beds around the Myall Lakes and concluded that only the glacial stage of the Kuttung Series was developed. He gave a thickness of 6,500 feet to this stage. He calculated a thickness of 25,000 feet for the "Burindi" Series (i.e. Upper and Lower Burindi).

Only the Lower and possibly some of the Upper Burindi beds were examined by the writer along the northern shores of Myall and Smith's Lakes. Lower Burindi beds, probably a continuation of those at O'Sullivan's Gap, were crossed before Mayer's Flat was reached. Conglomerates are conspicuous in association with tuffs between here and Bungwahl. According to Carey (1934*b*, p. 42), an anticlinal axis occurs at Bibby Harbour on the south side of the lake. This does not appear to continue on the northern side, since the dip from Mayer's Flat to Bungwahl appears to be consistently to the south-west. At Bungwahl mudstones containing marine fossils dip in a direction 250 degrees at 20°.

On the northern side of Smith's Lake, three miles from Bungwahl, the dip is 220 degrees at 60°.

From Elizabeth Bay rhythmically-bedded mudstones and tuffs dipping generally south-west are seen in the adjacent headlands.

An interesting tuffaceous conglomerate occurs near the Elizabeth Bay turnoff beside Lake Forster. The position of this in the sequence was not determined.

Forster.

Carboniferous strata are responsible for the formation of Cape Hawke, Bennett's Head, and the hills near Forster.

J. E. Carne (1896) recorded fossils from near the Signal Station at Forster, which were identified by W. S. Dun as follows: *Chonetes* sp. (closely allied to *C. hardrensis*), *Productus semireticulatus* Martin, *Spirifera*, *Gosseletina australis* Eth. fil., *Fenestella*, *Orthoceras*, corals (dendroid branching forms), *Bellerophon*, *Entolium* ?, Knorria.

Cyrtina carbonaria var. *australasica* Eth. fil. had already been recorded by Mr. Etheridge.

The writer independently came upon what was probably the same locality on the eastern end of the headland and collected the following forms: *Chonetes* sp. cf. *C. hardrensis* Phillips, *Productus* sp. cf. *semireticulatus* Martin, *Pelecypod* indet., *Monilopora nicholsoni*, *Calamites* (Australian Museum Collection, Nos. F38101–6; F38115–7; F38064).

Mr. Fletcher, who identified the fossils, suggested that they might be Upper Carboniferous, but the sediments in which they occur are fine-grained tuffs and mudstones which are more characteristic of the Lower Burindi Series.

B. SUMMARY OF THE CARBONIFEROUS SEQUENCE.

Further detailed mapping must be done before an accurate sequence for the Carboniferous beds is obtained. In the meantime, however, a tentative generalized section is submitted as follows:

	Max. Thickness. Feet.
Upper Kuttung Series.	
The Gloucester Rhyolites	1,500
Tuffs and mudstones with occasional conglomerate bands (Zone Y)	800
Upper Burindi (= Lower Kuttung) Series.	
Mudstones and tuffs with abundant marine fossils in some bands (Zone X)	3,000
Lava flow	250
Tuffs (Zone W)	800
Lava flow	400
Lower Burindi Series.	
Marine mudstones and tuffs with thin bands of conglomerate (Zone V)	1,000
Oolitic limestone	20
Marine mudstones (Zone U)	80
Oolitic limestone	30
Marine mudstones and tuffs with subordinate limestones and conglomerates	6,000
Tugrabakh Creek crinoidal limestone (Zone T)	200
Marine mudstones, tuffs and conglomerates	500
Total	14,580 plus

It will be seen that, in general, this sequence is in accord with that given by Sussmilch (1921, p. 242). In dividing it into three series, the writer has followed the lead of Carey and Browne (1938, p. 597).

The No. 1 lava flow has been omitted because it was not observed in any other of the sections examined and because severe faulting is known to occur to the east of Barrington where Sussmilch observed this flow. Other lava flows occur at various places in the sequence, but, since they are discontinuous, they may be disregarded for the time being. That they are present in abundance is indicated by the sequence in the Mograni sector. In dealing with individual sections, the No. 2 and No. 3 lava flows mentioned by Sussmilch are given these numbers since they are continuous for some distance and are indicated on his map.

The mudstones, tuffs, conglomerates and limestones which comprise the greater part of the Lower Burindi Series have been grouped together and an estimated thickness of 6000 feet has been assigned to them. In this group are included the O'Sullivan's Gap, Forster, Dungog and other beds.

The Tugrabakh Creek crinoidal limestone is mentioned, since it probably occurs near the base of the Lower Burindi Series. Since the junction between Carboniferous and Devonian beds has not been decided upon, the exact thickness of beds below the limestone and above the Barraba Series is not known.

C. PALAEONTOLOGY.

Fossil collecting in the area has been done hurriedly in every instance so that few generalizations with regard to the faunal distribution are justified at the moment. The lists of forms collected to date are as follows:

Upper Kuttung Series.

Zone Y.

Sussmilch collected: *Rhacopteris intermedia*, (?) *Rhacopteris ovata*, *Cardiopteris polymorpha*, *Archaeopteris* sp. ind., Calamitean stems.

Upper Burindi (= Lower Kuttung) Series.

Zone X.

Fenestella spp., Crinoid stems, *Spirifer pinguis* Sowerby, *Chonetes* cf. *papilionacea*, *Chonetes* cf. *hardrensis*, *Camarotoechia* cf. *pleurodon* Phillips, *Actinoconchus planosulcatus* Phillips, *Productus pustulosus* Phillips, *Productus barringtonensis* Dun, *Productus* sp. indet., *Spirifer* sp. indet., *Aviculopecten flexicostatus* Mitchell, indeterminate pelecypod, *Cordania gardneri* Mitchell.

At the top of the zone is a bed which contains a great abundance of *Productus pustulosus*, while the lowest bed is the prolific *Productus barringtonensis* horizon.

Zone W.

Orthis valida Dun, *Chonetes* sp., *Productus semireticulatus* Martin sp., *Productus* sp. indet., *Strophomena analoga* Phillips, ? *Actinoconchus planosulcatus* Martin sp.

Lower Burindi Series.

Zone V.

"*Leptaena analoga*" Phillips, *Productus* sp., *Spirifer pinguis* Sowerby, *Spirifer striata* Sowerby.

Zone U.

Chonetes aspinosa Dun, *Productus pustulosus* Martin, *Productus semireticulatus* Martin sp., *Spirifer pinguis* Sowerby, *Spirifer striata* Sowerby.

Spirifer horizon.—This is characterized by large numbers of the brachiopods, *Spirifer pinguis* and *Spirifer striata*. It occupies a high position in the Lower Burindi Series at O'Sullivan's Gap and may well be identical with Zone U. In

addition to the spirifers, the following forms were collected: "*Leptaena analoga*", *Chonetes* cf. *hardrensis*, *Fenestella* sp., *Productus* sp., Crinoid stems.

Gastropod horizon.—This may be of local occurrence. Only the one form, probably *Platyschisma depressa* Dana, was collected.

Tugrabakh Creek Limestone horizon (Zone T).—This horizon is characterized by the great abundance of crinoid stems and by the coral fauna—*Amygdalophyllum*, *Michelinia*, *Zaphrentis* sp., and *Syringopora* or *Cladochonus*. In associated mudstone the trilobite *Cordania gardneri* occurs.

The zones U, V, W and X were given the letters merely as a temporary device for reference purposes. Horizons within the zones are indicated by means of numbers, e.g. X1, X2, and X3. The letters have no other significance.

Sussmilch (1921, pp. 245–246) grouped all the marine fossils of the Upper and Lower Burindi and, in addition to some of those mentioned above, records *Dielasma sacculus*, *Orthis australis*, *Orthotetes crenistria*, *Spirifer crassa*, *Reticularia* and *Phillipsia* sp. indet.

Definite Lower Burindi forms, in addition to those included in that series, are *Gosseletina australis* Eth. fil., *Orthoceras* sp., *Bellerophon* sp., *Entolium* ?, *Cyrtina carbonaria* var. *australasica* Eth. fil., and *Monilopora nicholsoni* which come from Forster.

Devonian.

The Devonian rocks in the neighbourhood of Copeland were described by Sussmilch (1921, pp. 237–240). The same writer and W. N. Benson (1916) also examined and described the beds between Gloucester and Mount George, and agreed that representatives of the Tamworth and Barraba Series probably were present.

Reference to similar rock types was made by the writer (Voisey, 1938, 1939*a*, 1939*b*), but it has not been possible to separate the two series from one another up to the present time. Indeed, it is a matter of great difficulty to separate the Devonian from the Carboniferous strata.

Banded claystones and tuffs almost certainly belonging to the Tamworth Series are exposed by the Pacific Highway between Krambach and Brushy Mountain. Hard tuff bands are conspicuous in the series and have given rise to hilly country.

Between Krambach and Bunyah banded olive-green mudstones are interbedded with massive bluish-grey tuffs which, in places, outcrop as heaps of boulders which may be followed for some distance. Near Bunyah they have resisted erosion to the extent of forming parallel ridges running generally east and west. These rocks give way to those of Lower Carboniferous age between Bunyah and Gloucester.

The Devonian rocks extend eastwards to the margin of the coastal plains or lagoons. Evidence of their presence at the bridge over Wang Wauk river was demonstrated to the writer by Dr. G. D. Osborne in 1930. Dr. Osborne found *Lepidodendron australe* in the mudstones beside the bridge.

Conclusion.

The bearing which the geology of the Gloucester District has upon the study of the Upper Palaeozoic Stratigraphy of New South Wales will be discussed in a later publication. It is of interest to note that an increased number of marine fossils are now known from beds which are the equivalents of the terrestrial Lower Kuttung Series.

Acknowledgements.

The writer is indebted to Dr. W. R. Browne and Dr. G. D. Osborne of the University of Sydney, and Dr. S. W. Carey of the Australasian Petroleum Company for their helpful discussions.

Mr. H. O. Fletcher of the Australian Museum has identified and catalogued most of the fossils mentioned in this paper. Dr. Dorothy Hill named the corals. To these two palaeontologists my thanks are due.

In addition to the above, I desire to thank Mr. J. McInnes and Miss McInnes of Barrington for their hospitality, and Mr. Fordyce of Gloucester for giving me some very useful information about the district.

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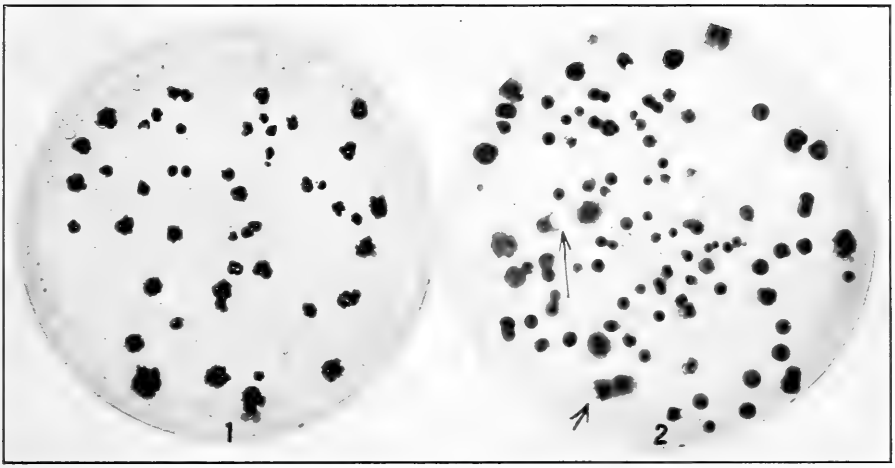
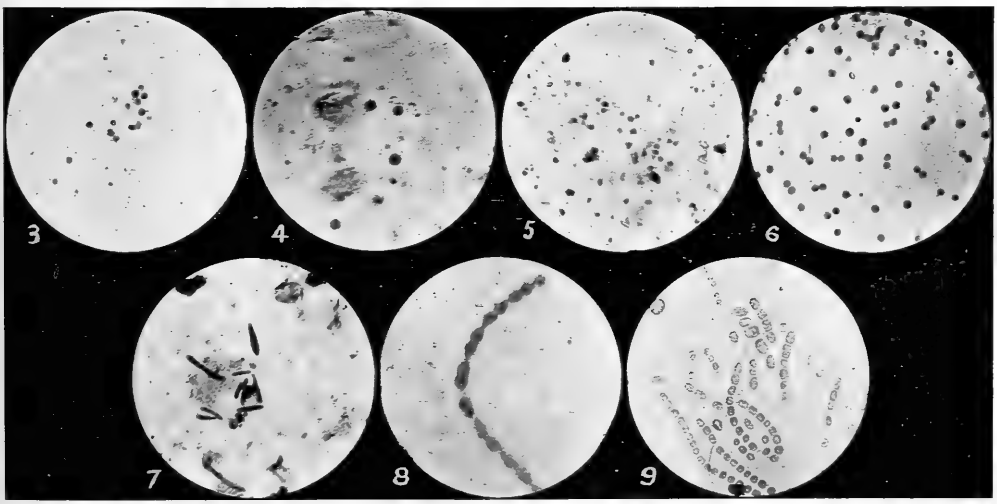
EXPLANATION OF PLATE V.

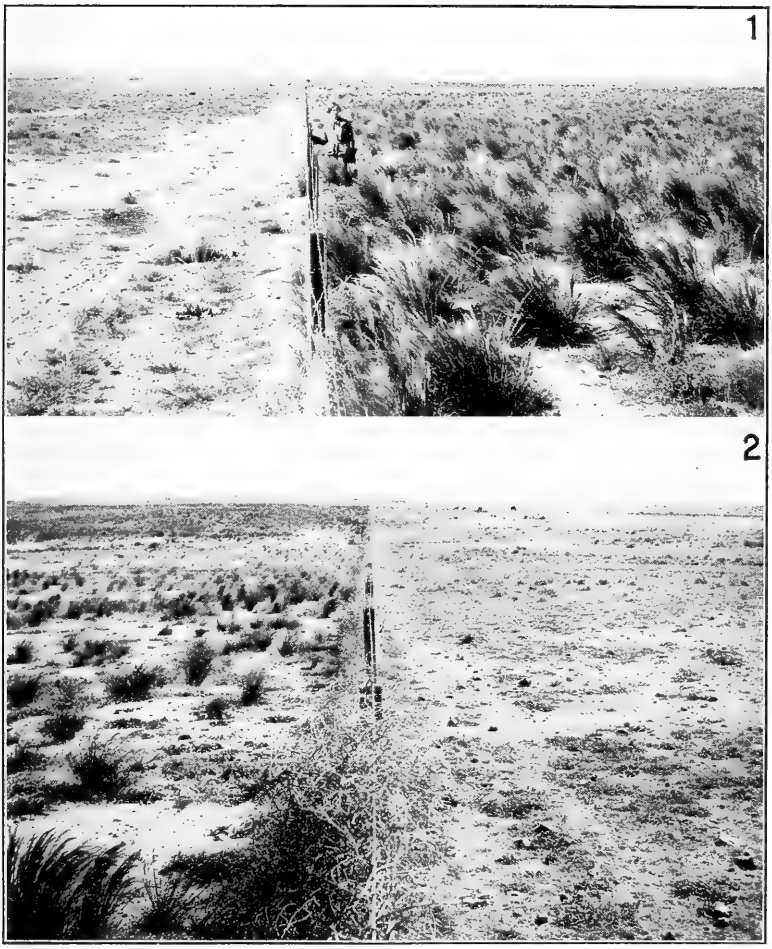
Geological Map of the Country between the Manning and Karuah Rivers, N.S.W.

Note.—In the legend to the map, the Tugrabakh Creek Limestone is marked as Devonian in error. It should be Carboniferous.

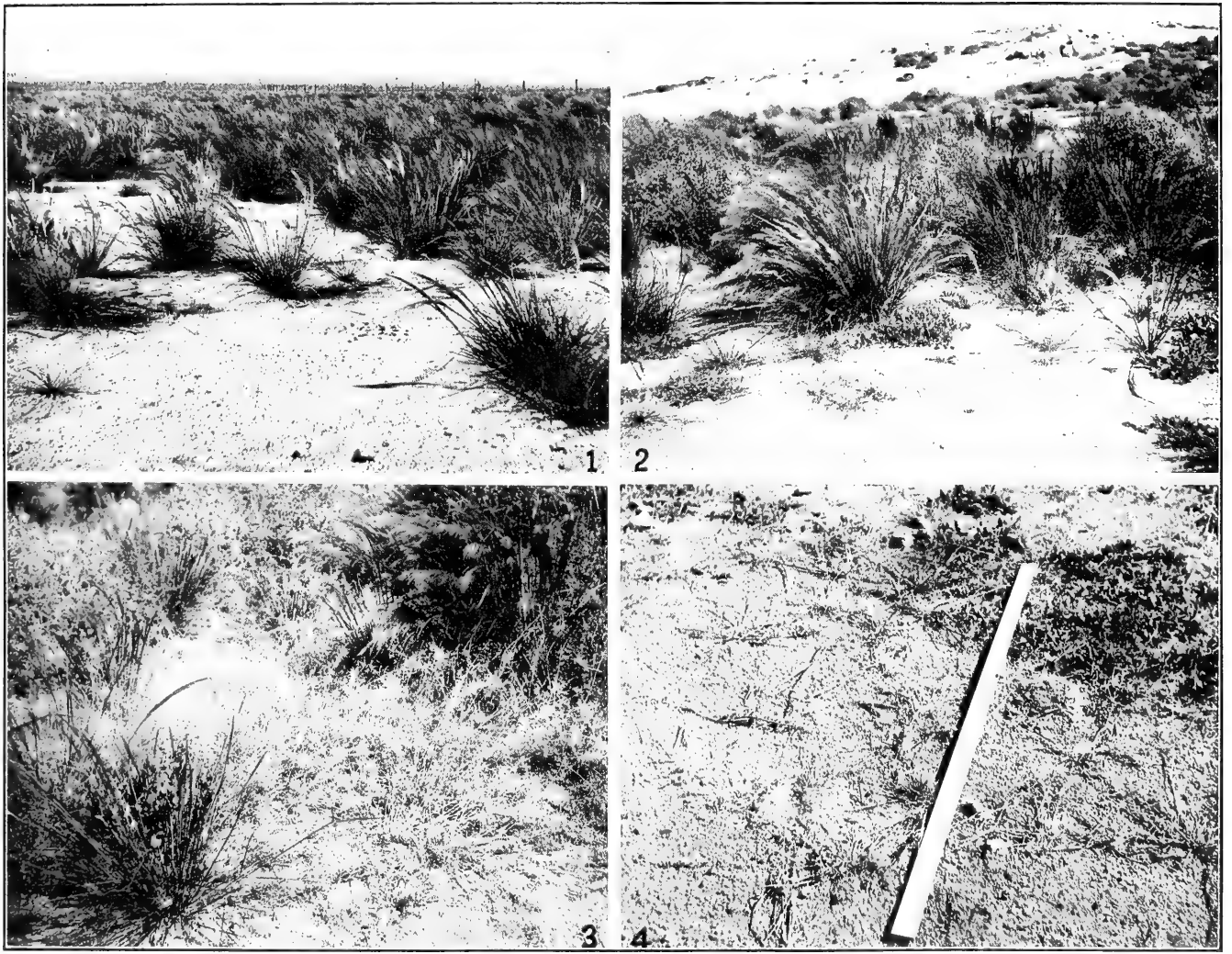




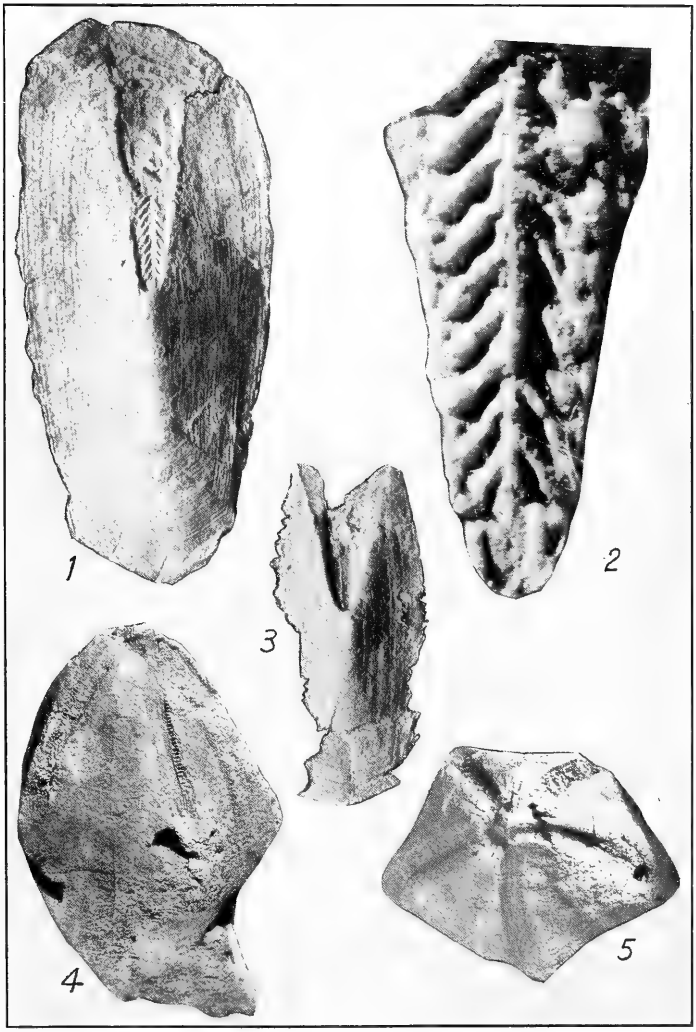
1, 2, 6, *Azotobacter*; 3-5, *Azotobacter*-like organisms; 7, Clostridia; 8, 9, Blue-green algae.



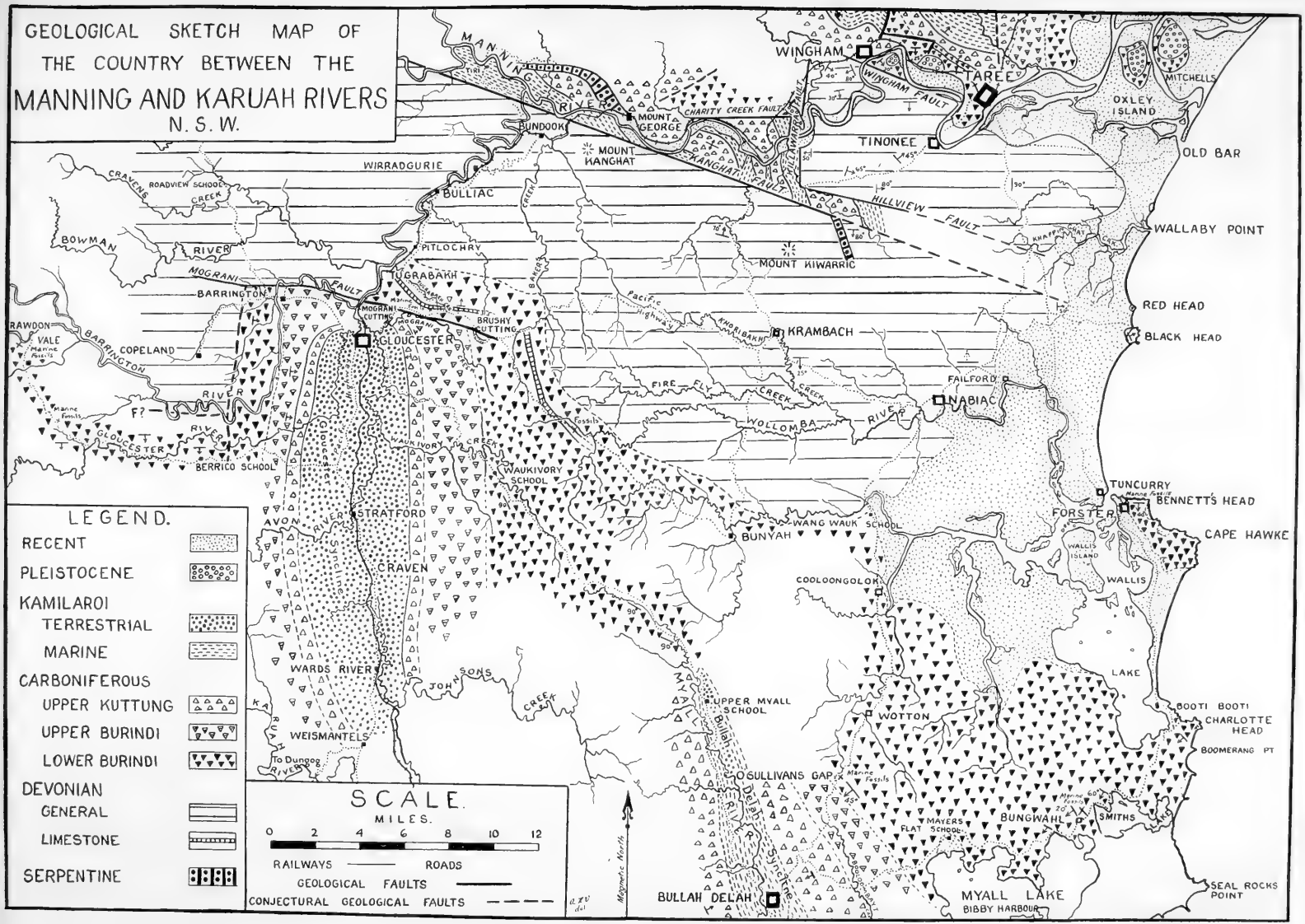
Plant regeneration at Broken Hill.



Plant regeneration at Broken Hill.



Permian Blastoids from New South Wales.


GEOLOGICAL SKETCH MAP OF THE COUNTRY BETWEEN THE MANNING AND KARUAH RIVERS N. S. W.
LEGEND.
RECENT
PLEISTOCENE
KAMILAROI
TERRESTRIAL
MARINE
CARBONIFEROUS
UPPER KUTTUNG
UPPER BURINDI
LOWER BURINDI
DEVONIAN
GENERAL
LIMESTONE
SERPENTINE
SCALE
MILES.
0 2 4 6 8 10 12
RAILWAYS ROADS
GEOLOGICAL FAULTS
CONJECTURAL GEOLOGICAL FAULTS
Magnetic North
MANNING RIVER
WINGHAM
TAREE
WINGHAM FAULT
MITCHELLS
OXLEY ISLAND
OLD BAR
TINONEE
MOUNT GEORGE
CHARITY CREEK FAULT
BUNDOOK
MOUNT KANGHAT
KANGHAT FAULT
HILLVIEW FAULT
WALLABY POINT
RED HEAD
BLACK HEAD
MOUNT KIWARRIC
WIRRADGURIE
BULLIAC
CRAVENS CREEK
ROADVIEW SCHOOL
BOWMAN RIVER
PITLOCHRY
MOGRANI FAULT
BARRINGTON
GRABAKH
MOGRANI CUTTING
BRUSHY CUTTING
KRAMBACH
GLOUCESTER
COPELAND
RAWDON VALE
BARRINGTON RIVER
FIRE FLY CREEK
FAILFORD
NABIAC
WOLLOMBA RIVER
BERRICO SCHOOL
GLOUCESTER RIVER
WAUKIVORY CREEK
WAUKIVORY SCHOOL
TUNCURRY
BENNETT'S HEAD
FORSTER
CAPE HAWKE
WANG WAUK SCHOOL
BUNYAH
AVON RIVER
STRATFORD
CRAVEN
WALLIS ISLAND
WALLIS
COOLOONGOLOK
WARDS RIVER
JOHNSONS CREEK
LAKE
BOOTI BOOTI
CHARLOTTE HEAD
BOOMERANG PT
UPPER MYALL SCHOOL
WOTTON
WEISMANTELS
To Dungog
O'SULLIVANS GAP
MAYERS FLAT SCHOOL
BUNGWAHL
SMITHS
SEAL ROCKS POINT
BULLAH DELAH
MYALL LAKE
BIBBY HARBOUR

THE FOOD-PLANTS OR HOSTS OF SOME FIJIAN INSECTS. IV.

By William Greenwood.

(*Communicated by Dr. A. B. Walkom.*)

[Read 29th May, 1940.]

This paper contains a number of new records which have been obtained since Part iii appeared (These Proceedings, liv, 1929, 344). Thanks are due to the authorities at the Imperial Institute of Entomology for most of the insect identifications and at the Royal Botanic Gardens, Kew, for naming some of the plants.

Credit for the various records is given by initials as follows: W. Greenwood (W.G.), C. Knowles (C.K.), A. Lea (A.L.), R. Lever (R.L.), R. Paine (R.P.), H. Phillips (H.P.), H. Simmonds (H.S.), T. Taylor (T.T.), R. Veitch (R.V.).

The records credited to Mr. H. Phillips have been seen and verified by the writer. All records, except those credited to Phillips, Veitch and Greenwood, have been taken from various publications.

During recent years the names of a number of common tropical plants have been altered. In such cases the writer has adhered to the name used in previous articles of this series.

Lepidoptera.

Except where otherwise stated, the records for Lepidoptera refer to the feeding habits of the larva.

Nymphalidae: *Doleschalia bisalta* Cram. Eats the leaves of the following Acanthaceae: *Eranthemum laxiflorum* A. Gray and *Graptophyllum pictum* L. (both H.S.).

Lycaenidae: *Nacaduba biocellata* Feld. Feeds on flower heads of *Acacia Farnesiana* Willd. (Leguminosae) (H.P.).

Sphingidae: *Herse convolvuli* L. Feeds on leaves of *Ipomoea Bona-nox* L. (Convolvulaceae) (W.G.).

Arctiidae: *Utetheisa pulchella* L. Skeletonizing leaves of *Tournefortia argentea* L.f. (Boraginaceae) (H.P.).

Geometridae: *Casbia alphitoniae* L. B. Prout. Feeds on leaves of *Alphitonia zizyphoides* A. Gray. (Rhamnaceae) (H.P.).—*Thalassodes pilaria* Gn. Eats the leaves of *Eugenia Jambos* L. (Myrtaceae) (W.G.).—*Colutoceras cheramota* Meyr. Eats the leaves of *Nelitris vitiensis* A. Gray. (Myrtaceae) (W.G.).—*Anisodes compacta lautokensis* L. B. Prout. Feeds on the leaves of *Nelitris vitiensis* A. Gray. (Myrtaceae) (W.G.).—*Gymnoscelis minutissima* Swinh. Feeds on the leaves of *Nelitris vitiensis* A. Gray. (Myrtaceae) (H.P.).—*Cleora munditibia* L. B. Prout. Feeds on leaves of *Mucuna aterrima* Holland. (Leguminosae) (W.G.).

Noctuidae: *Anomis fulvida xanthochroa* Butl. Eats the leaves of *Hibiscus tiliaceus* L. (Malvaceae) (H.P.).—*Hyblaea sanguinea* Gaede. Folds and feeds on leaves of *Premna taitensis* Schauer. (Verbenaceae) (W.G.).—*H. puera* Cram.

Folds and feeds on leaves of *Vitex trifolia* L. (Verbenaceae) (H.P.).—*Phlegetonia delatrix* Guen. Feeds on leaves of the following Myrtaceae: *Eugenia Jambos* L. (W.G.) and *Nelitris vitiensis* A. Gray (H.P.).—*Phytometra chalcites* Esp. Eats the leaves of the following Leguminosae: *Pueraria Thunbergiana* Benth. (H.P.), *Clitorea Ternatea* L. (W.G.) and *Vigna Catiang* Walp. (H.P.); also eats the flowers of *Solanum torvum* Sw. (Solanaceae) (H.P.).—*Amyna octo* Guen. Feeds on leaves of *Cardiospermum halicacabum* L. (Sapindaceae) (W.G.).—*A. natalis* Wlk. Feeds on leaves of *Malvastrum tricuspidatum* A. Gray (Malvaceae) (W.G.) and *Amaranthus viridis* L. (Amarantaceae) (H.P.).—*Rhesala albizziae* A. E. Prout. Eats the leaves of *Albizzia Lebbek* Benth. and *A. procera* Benth. (Leguminosae) (both W.G.).—*Heliothis obsoleta* Fab. Feeds on buds and flowers of *Antirrhinum majus* L. (Scrophulariaceae) (W.G.), leaves of *Coleus Blumei* Benth. (Labiateae) (W.G.), leaves of *Zinnia elegans* Jacq. (Compositae) (W.G.), flower heads of *Tagetes patula* L. (Compositae) (W.G.), green pods of *Pisum sativum* L. (Leguminosae) (H.P.) and fruits of *Nicotiana Tabacum* L. (Solanaceae) (H.S.).—*H. assulta* Guen. Feeds on flower heads of *Tithonia diversifolia* Hemsl. (Compositae) (H.P.).—*Mocis trifasciata* Steph. Eats the leaves of *Pueraria Thunbergiana* Benth. (Leguminosae) (W.G.).—*Earias huegeli* Rogenh. Eats the fruits of *Urena lobata* L. (Malvaceae) (W.G.) and of *Triumfetta rhomboidea* Jacq. (Tiliaceae) (W.G.).—*Eublemma rivula* Moore. Feeds in the flower heads of *Vernonia cinerea* Less. (Compositae) (H.P.).—*E. anachoresis* Wllg. Eats the leaves of *Waltheria americana* L. (Sterculiaceae) (W.G.).—*Achaea janata* L. Feeds on flowers of *Punica granatum* L. (Lythraceae) (H.P.).—*Grammodes oculicola* Wlk. Eats the leaves of *Phyllanthus Ferdinandi* Mull-Arg. (Euphorbiaceae) (W.G.).—*Nanaguna breviuscula* Wlk. Feeds on the flowers of *Desmodium umbellatum* DC. (Leguminosae) (W.G.).—*Ericeia levuensis* A. E. Prout. Feeds on leaves of *Cassia fistula* L. (Leguminosae) (H.P.).—*Othreis fullonica* L. Eats the leaves of *Erythrina fusca* Lour. (Leguminosae) (H.P.).—*Parallelia anetica* Fldr. Eats the leaves of *Nelitris vitiensis* A. Gray (Myrtaceae) (W.G.).—*Agrotis ypsilon* Rott. Feeds on *Nicotiana Tabacum* L. (Solanaceae) (R.L.).

Pyralidae: *Nacoleia diemenalis* Gn. Eats the leaves of *Phaseolus aconitifolius* Roxb. (Leguminosae) (W.G.).—*Maruca testulalis* Hb. Feeds on the following Leguminosae: green pods of *Crotalaria striata* DC. (H.P.), green pods of *Canavalia gladiata* DC. (W.G.) and leaves of *Phaseolus Mungo* L. (W.G.).—*Terastia meticulosalis* Gn. Tunnels in shoots of *Erythrina fusca* Lour. (Leguminosae) (W.G.).—*Botyodes asialis* Gn. Feeds on leaves of *Casearia disticha* A. Gray (Samydaceae) (H.P.).—*Hypargyria metalliferella* Rag. Eats the leaves and flowers of *Celastrus Richii* A. Gray (Celastrinae) (W.G.).—*Margaronia marinata* F. Eats the leaves of *Guettarda speciosa* L. (Rubiaceae) (H.P.).—*M. oceanitis* Meyr. Feeds on the leaves of *Ervatamia orientalis* Turrill (Apocynaceae) (H.P.).—*M. indica* Saund. Feeds on leaves of the following Cucurbitaceae: *Cucumis sativus* L. (R.L.), *Sechium edule* Sw. (W.G.), *Momordica Charantia* L. (W.G.) and *Citrullus vulgaris* Schrad. (W.G.).—*Pagyda tremula* Meyr. Eats the leaves of *Premna taitensis* Schauer. (Verbenaceae) (H.P.).—*Rehimena phrynealis* Wlk. Feeds in green fruits of *Kleinhovia hospita* L. (Sterculiaceae) (W.G.).—*Striglina superior* Butl. Eats the leaves of *Cassia fistula* L. (Leguminosae) (H.P.).—*Ceratagra mitrophora* Meyr. Feeds on young leaves of *Catha vitiensis* Seem. (Celastrinae) (W.G.).—

Homoeosoma symmicta Meyr. Feeds in flower heads of *Erigeron floribundus* (H.B.K.) Schult.-Bip. (Compositae) (W.G.).—*H. hypogypsa* Meyr. Feeds in flower heads of *Vernonia cinerea* Less. (Compositae) (W.G.).—*Myelois pectinicornella* Hmps. Feed in pods of the following Leguminosae: *Erythrina indica* Lam. (H.P.) and *Bauhinia monandra* Kurz. (W.G.).—*Thiallela rhodoptila* Meyr. Eats the leaves of *Alphitonia zizyphoides* A. Gray (Rhamnaceae) (W.G.).—*Tirathaba trichogramma* Meyr. Feeds on the flowers of the following Palmae: *Pritchardia pacifica* Seem. and *Oreodoxa regia* Humbt. (both R.P.).—*Cryptoblabes plagioleuca* Turn. Feeds on flowers of *Eriobotrya japonica* Lindl. (Rosaceae) (W.G.), young leaves of *Inocarpus edulis* Forst. (Leguminosae) (H.P.), green fruits of *Ricinus communis* L. (Euphorbiaceae) (W.G.) and green fruits of *Vitex trifolia* L. (Verbenaceae) (H.P.).—*Salebria ferrorubella* Wlk. Eats the flowers of *Dysoxylon Richii* (A. Gray) Seem. (Meliaceae) (W.G.).—*Phalobathra escigera* Meyr. Eats the leaves of *Celastrus Richii* A. Gray (Celastrinae) (W.G.).—*Omiodes vulgaris* Gn. Feeds on the leaves of *Alternanthera sessilis* R.Br. (Amarantaceae) (W.G.).—*Etiella drososcia* Meyr. Feeds in ripe pods of *Crotalaria striata* DC. (Leguminosae) (W.G.).—*E. behri* Zell. Feeds in ripe pods of the following Leguminosae: *Crotalaria striata* DC. and *Erythrina indica* Lam. (both H.P.).—*Ercta ornatalis* Dup. Eats the leaves of *Ipomoea pes-caprae* Sw. (Convolvulaceae) (H.P.).—*Ephestia cautella* Wlk. Feeds on dried peaches (H.P.), raisins and stored copra (both R.L.).—*Chilo simplex* Butl. Feeds in stalks of *Oryza sativa* L. (Gramineae) (W.G.).—*Heortia vitessoides* Moore. Larvae feed in swarms on leaves of *Phaleria lanceolata* Gilg. (Thymeleaceae) (W.G.).—*Crocidolomia binotalis* Zell. Feeds on leaves of *Brassica oleracea* L. (Cruciferae) (R.L.).—*Nephopteryx exotypa* Meyr. Webs together and skeletonizes the leaves of *Pleiogyrum Solandri* Engl. (Anacardiaceae) (W.G.).

TINEIDAE: *Batrachedra arenosella* Wlk. Feeds on inflorescence of *Cocos nucifera* L. (Palmae) (T.T.).—*B. atriloqua* Meyr. Feeds on the inflorescence of *Cocos nucifera* L. (Palmae) (T.T.).—*Hellula undalis* F. Eats the leaves of *Brassica campestris* L. (Cruciferae) (R.L.).—*Setomorpha rutella* Zell. Feeds on leaves of *Psidium Guayava* L. (Myrtaceae) (R.L.).—*Aeolarchis sphenotoma* Meyr. Feeds on surface of leaves of *Pandanus caricosus* Rumph. (Pandanaceae) (R.L.).

LYONETIADAE: *Decadarchis heterogramma* Meyr. Larvae feed in old dry pods of *Bauhinia monandra* Kurz. (Leguminosae) and in dead stems of *Zea Mays* L. (Gramineae) (both W.G.). Bred from pupae of *Tirathaba trichogramma* Meyr. (Pyralidae) (R.P.).—*D. flavistriata* Wals. Feeds in decaying timber (H.P.).—*D. psammaula* Meyr. Feeds on leaves of *Cocos nucifera* L. (Palmae) (R.L.).—*Opogona citrinodes* Meyr. Feeds in rotten pods of *Mucuna aterrima* Holland (Leguminosae) (W.G.).—*O. regressa* Meyr. Feeds on flowers of *Cocos nucifera* L. (Palmae) (R.P.) and in the fruits of *Inocarpus edulis* Forst. (Leguminosae) (R.L.).

GRACILARIADAE: *Gracilaria palaearcha* Meyr. Rolls and feeds on leaves of *Phyllanthus Ferdinandi* Mull-Arg. (Euphorbiaceae) (H.P.).—*G. xanthopharella* Meyr. Feeds on leaves of *Phyllanthus Ferdinandi* Mull-Arg. (Euphorbiaceae) (H.P.).

HYPONOMEUTIDAE: *Ethmia colonella* Wals. Eats the leaves of *Cordia subcordata* Lam. (Boraginaceae) (H.P.).

GLYPHIPTERYGIDAE: *Simaethis chalcotoxa* Meyr. Feeds on the leaves of *Ficus Barclayi* Seem. (Urticaceae) (W.G.).

HELIODINIDAE: *Stathmopoda trichrysa* Meyr. Feeds in dry pods of following Leguminosae: *Bauhinia monandra* Kurz. and *Caesalpinia pulcherrima* Sw. (both W.G.).

COSMOPTERYGIDAE: *Labdia calida* Meyr. Feeds on seeds in ripe pods of *Caesalpinia pulcherrima* Sw. and *C. Bonduc* Roxb. (Leguminosae) (both W.G.).—*Ascalenia thoracista* Meyr. Feeds on flowers of *Albizzia Lebbek* Benth. and *A. procera* Benth. (Leguminosae) (both W.G.).—*Pyroderces paroditis* Meyr. Feeds on inflorescence of *Cocos nucifera* L. (Palmae) (T.T.).

COLEOPHORIDAE: *Coleophora immortalis* Meyr. Feeds on inflorescence of *Amaranthus viridis* L. (Amarantaceae) (W.G.).

PHYLLORYCTERIDAE: *Cyphosticha coerulea* Meyr. Feeds under epidermis of leaves of following Leguminosae: *Canavalia gladiata* DC., *Dolichos Lablab* L. and *Atylosia scarabaeoides* Benth. (all W.G.).

EUCOSMIDAE: *Argyroploce illepida* Butl. Feeds on fruits of *Colubrina asiatica* Brongn. (Rhamnaceae) (W.G.).—*Spilonota holotephras* Meyr. Eats the young leaves of the following Myrtaceae: *Nelitris vitiensis* A. Gray, *Eugenia rivularis* Seem., *Metrosideros polymorpha* Gaud. and *Eucalyptus maculata* Hook. var. *citriodora* Hook. (all W.G.).

TORTRICIDAE: *Adoxophyes fasciculana* Wlk. Eats the leaves of *Enterolobium Saman* Prain (Leguminosae) (W.G.), *Jasminum didymum* Forst. (Oleineae) (H.P.) and *Psidium Guayava* L. (Myrtaceae) (R.L.).

PTEROPHORIDAE: *Sphenarches caffer* Zell. Feeds on flowers of *Antirrhinum majus* L. (Scrophulariaceae) (W.G.) and on leaves of *Lagenaria vulgaris* Ser. (Cucurbitaceae) (H.P.).

GALLERIIDAE: *Meliphora grisella* F. Feeds on shelled walnuts (W.G.).—*Corcyra cephalonica* Staint. Found feeding in dried apples from Australia (H.P.).

COLEOPTERA.

The records for Coleoptera refer to the feeding habits of the larva unless otherwise stated.

CUCUJIDAE: *Oryzaephilus surinamensis* L. Feeds in stored rice, coconut meal and peach stones (R.L.).

NITIDULIDAE: *Haptonchus tetragonus* Murr. Feeds on ripe damaged fruits of *Ananas sativus* Schult. f. (Scitamineae) (W.G.).

COCCINELLIDAE: *Epilachna 28-punctata* F. Both larva and imago feed on leaves of *Cucumis sativus* L. (Cucurbitaceae) (R.L.).—*Cryptolaemus montrouzieri* Muls. Both larva and imago feed on Coccidae generally (A.L.).—*Cryptognatha nodiceps* Mshl. Both larva and imago feed on *Aspidiotus destructor* Sign. and *Diaspis pentagona* Targ. (Coccidae) (both T.T.).—*Chilocorus nigritus* F. var. Imago feeds on *Aspidiotus destructor* Sign. (Coccidae) (R.P.).

CLERIDAE: *Necrobia rufipes* de Geer. Larvae feed in rice bran (R.L.).

PTINIDAE: *Cathorama herbarium* Gorh. Larvae bore in books (R.L.).

TENEBRIONIDAE: *Tribolium castaneum* Hbst. Feed in stored Rice (R.L.).—*T. ferrugineum* F. Feed on stored rice (R.L.).—*Alphitobius laevigatus* F. Feed in rice bran (R.L.).

RUTELIDAE: *Adoretus versutus* Har. The imago eats the leaves of *Zinnia elegans* Jacq. (Compositae) and *Acalypha Wilkesiana* Mull-Arg. (Euphorbiaceae) (both W.G.).

SCARABIDAE: *Coprus incertus* L. var. *prociduus*. Feeds on larvae of *Musca domestica* L. (Muscidae) (H.S.).

CERAMBYCIDAE: *Oopsis mutator* F. Feeds on seeds in pods of *Erythrina indica* Lam. (Leguminosae) (H.P.).—*Olethrius scabripennis* F. Bores in stems of *Bruguiera Rheedii* Bl. and *Rhizophora mucronata* Lam. (Rhizophoraceae) (both W.G.).

HALTICIDAE: *Aphthona veitchi* Bryant. Imago feeds on leaves of *Euphorbia chamissonis* Boiss. (Euphorbiaceae) (W.G.).

GALERUCIDAE: *Aulacophora argyrogaster* Montr. Imago eats the leaves of *Cucumis Melo* L. (Cucurbitaceae) (W.G.).—*A. coffaea* Horn. Imago eats the leaves of the following Cucurbitaceae: *Cucumis sativus* L. and *Cucurbita Pepo* DC. (both R.L.).

HISPIDAE: *Promecotheca reichei* Baly. All stages feed on leaves of *Pritchardia pacifica* Seem. (Palmae) (R.P.).

BRUCHIDAE: *Pachymerus gonager* F. Feeds in ripe pods of *Bauhinia monandra* Kurz. (Leguminosae) (W.G.).

SCOLYTIDAE: *Xyleborus perforans* Woll. Found boring in trunks of *Cocos nucifera* L. (Palmae) (R.P.).—*X. morstatti* Hag. Found boring in stems of *Persea gratissima* Gaertn. (Lauraceae) (R.P.).

PLATYPIDAE: *Platypus gerstaeckeri* Chap. Bores in timber of *Podocarpus vitiensis* Seem. (Coniferae) (R.L.).

ANTHRIBIDAE: *Araecerus fasciculatus* de Geer. Feed on seeds in pods of *Caesalpinia pulcherrima* Sw. (Leguminosae) (W.G.).

CURCULIONIDAE: *Elytroteinus subtruncatus* Fairm. Bores in stems of garden Begonia (Begoniaceae) (H.S.).

HYMENOPTERA

The records for Hymenoptera refer to the feeding habits of the larva.

ICHNEUMONIDAE: *Ecthromorpha diversor* Morl. Parasitic on larva of *Botyodes asialis* Gn. (Pyralidae) (H.P.) and on pupa of *Tirathaba trichogramma* Meyr. (Pyralidae) (T.T.).—*E. tirathabae* Perk. Bred from pupae (?) of *Tirathaba trichogramma* Meyr. (Pyralidae) (T.T. and R.P.).—*Nemeritis palmaris* Wilk. Parasitic on *Tirathaba trichogramma* Meyr. (Pyralidae) (R.L.).

BRACONIDAE: *Meteorus trichogrammae* Wilk. Parasitic on larva of *Tirathaba trichogramma* Meyr. (Pyralidae) (T.T.).—*Phaenocarpa leveri* Nixon. Bred from larvae of *Dacus passiflorae* Frogg. (Trypetidae) (R.L.).—*Macrocentrus calacte* Nixon. Bred from larvae of *Argyroploce illepida* Butl. (Tortricidae) (R.L.).—*Biosteres tryoni* Cam. Parasitic on larvae of *Dacus passiflorae* Frogg. (Trypetidae) (R.L.).—*Opius fletcheri* Silv. Parasitic on larvae of *Dacus passiflorae* Frogg. (Trypetidae) (R.L.).—*Apantales tirathabae* Wilk. Parasitic on larva of *Tirathaba trichogramma* Meyr. (Pyralidae) (T.T.).

CHALCIDAE: *Brachymeria fijiensis* Ferr. Parasitic on *Platyedra gossypiella* Saund. (Gelechiidae) (H.S.) and *Agonoxena argaula* Meyr. (Coleophoridae) (H.S.).—*Antrocephalus renalis* Waterst. Bred from pupae of *Tirathaba trichogramma* Meyr. (Pyralidae) (R.L.).—*Spalangia cameroni* Perk. Parasitic on pupae of *Dacus passiflorae* Frogg. (Trypetidae) and *Musca domestica* L. var. *vicina* Macq. (Muscidae) (both R.L.).

EULOPHIDAE: *Syntomosphyrum indicum* Silv. Parasitic on larvae of *Dacus passiflorae* Frogg. (Trypetidae) (R.L.).—*Aspidiotiphagus citrinus* Craw. Parasitic on *Diaspis rosae* Sandberg. (Coccidae) (C.K.).—*Pleurotropis parvulus* Ferr.

Parasitic on larvae and pupae of *Promecotheca reichei* Baly and *P. bicolor* Maulik (Hispidae) (both T.T.).—*Tetrastichus taylori* Ferr. Parasitic on *Elasmus hispidarum* Ferr. (Elasmidae) (T.T.).—*T. giffardianus* Silv. Parasitic on larvae and pupae of *Dacus passiflorae* Frogg. (Trypetidae) (H.S.).

ELASMIDAE: *Elasmus hispidarum* Ferr. Feeds on larva of *Promecotheca reichei* Baly (Hispidae) (T.T.).

TRICHOGRAMMATIDAE: *Oligosita utilis* Kow. Parasitic on eggs of *Promecotheca reichei* Baly (Hispidae) (T.T.).—*Trichogrammatoidea nana* Zehnt. Parasitic on larva of *Levuana iridescens* B-B. (Zygaenidae) (T.T.) and on eggs of *Tirathaba trichogramma* Meyr. (Pyralidae) (T.T.).

POMPILIIDAE: *Cyphononyx vitiensis* Turn. Imago stores its nest with paralysed Araneid spiders (W.G.).

HEMIPTERA.

The records for Hemiptera refer to all stages except where otherwise noted.

PENTATOMIDAE: *Vitellus insularis* St. On leaves and shoots of *Guioa rhoifolia* Radlk. (Sapindaceae) (W.G.).—*Brachyplatys pacifica* Dall. Feeds on leaves and shoots of *Erythrina fusca* Lour. (Leguminosae) (W.G.).—*Tectocoris lineola* F. Feeds on shoots of *Sterculia Guppyi* Greenwood (Sterculiaceae) (W.G.).

LYGAEIDAE: *Paromius pallidus* Montr. On inflorescence of *Dichanthium annulatum* Stapf (Gramineae) (W.G.).—*Graptostethus servus* F. var. Feeding on shoots of *Canavalia ensiformis* DC. (Leguminosae) (W.G.).—*Germalus pacificus* Kirk. Feeds on eggs and nymphs of *Teleonemia lantanae* Dist. (Tingidae) and on eggs of *Dacus passiflorae* Frogg. (Trypetidae) (both H.S.).

TINGIDAE: *Teleonemia lantanae* Dist. Leaves of *Lantana crocea* (Verbenaceae) (H.S.).

CAPSIDAE: *Orthotylus vitiensis* Kirk. On stems and leaves of *Premna taitensis* Schauer. (Verbenaceae) (W.G.).

DELPHACIDAE: *Sogota furcifera* Horv. Feeds on leaves and stems of *Oryza sativa* L. (Gramineae) (R.L.).

PSYLLIDAE: *Mesohomotoma hibisci* Frogg. On leaves of *Hibiscus tiliaceus* L. (Malvaceae) (H.P.).

APHIDAE: *Oregma iceryae* Laing. On *Miscanthus japonicus* Anderss. (Gramineae) (R.V.).—*Pentalonia nigronervosa* Coq. On *Musa sapientum* L. (Scitamineae) (original recorder's name unknown to the writer).

ALEURODIDAE: *Neomaskellia bergii* Sign. On underside of leaves of the following Gramineae: *Lepturus repens* R.Br. and *Urochloa paspaloides* Presl. (both W.G.).

COCCIDAE: *Icerya seychellarum* Westw. On stems of *Cinnamomum Zeylanicum* Breyn. (Lauraceae) and on pods of *Enterolobium Saman* Prain (Leguminosae) (both W.G.). Also on leaves of *Persea gratissima* Gaertn. (Lauraceae) (R.L.).—*I. purchasi* Mask. On stems of *Crotalaria striata* DC. (Leguminosae) (W.G.).—*Aulacaspis pentagona* T.T. Feeds on stems of the following Verbenaceae: *Stachytarpheta jamaicensis* Vahl. (H.S.), *S. mutabilis* Vahl. (W.G.) and *Verbena bonariensis* L. (W.G.).—*Chionaspis citri* Comst. On stems, leaves and fruit of *Citrus aurantium* L. var. *japonica* (Rutaceae) (W.G.).—*Vinsonia stellifera* Westw. On leaves of *Garcinia xanthochymus* Hook. (Guttiferae) (W.G.).—*Lecanium viride* Green. On *Ixora coccinea* L. (Rubiaceae) (W.G.).—*L. hemisphaericum* T.T. On pinnae of *Adiantum*

trapeziforme Sw. (Filices) (W.G.).—*Pseudococcus citri* Risso. On leaves of the following Urticaceae: *Pellionia elatostemoides* Gaud. and *P. filicoides* Seem. (both W.G.).—*Ceroplastes rubens* Mask. On stems *Asystasia gangetica* T. And., *Thunbergia fragrans* Roxb. and *T. erecta* Boj. (Acanthaceae) (all W.G.). On leaves *Barringtonia racemosa* Bl. (Lecythidaceae) (W.G.).—*Saissetia nigra* Nietn. On leaves *Canna indica* L. (Scitamineae), stems *Coleus amboinicus* Lour. (Labiateae), stems and leaves *Xanthium italicum* Moretti (Compositae), leaves of *Plumeria acutifolia* Poir. (Apocynaceae) (all W.G.).—*Aspidiotus destructor* Sign. On leaves of *Plumeria acutifolia* Poir. (Apocynaceae) (W.G.), *Piper* spp. (Piperaceae) (R.P.), *Cassia obtusifolia* L. (*C. Tora* L.) (Leguminosae) (R.P.), *C. occidentalis* L. (Leguminosae) (R.P.), leaves *C. nodosa* Buch-Ham. (Leguminosae) (W.G.), *Psidium Guayava* L. (Myrtaceae) (R.P.), *Mangifera indica* L. (Anacardiaceae) (R.P.), *Inocarpus edulis* Forst. (Leguminosae) (R.P.), *Spondias dulcis* Forst. (Anacardiaceae) (R.P.), *Aleurites triloba* Forst. (Euphorbiaceae) (R.P.), *Hevea brasiliensis* Mull-Arg. (Euphorbiaceae) (R.P.), *Wormia biflora* Seem. (Dilleniaceae) (R.P.), *Zingiber officinale* Rosc. (Scitamineae) (R.P.), leaves *Alpinia nutans* Rosc. (Scitamineae) (W.G.), *Tetranthera vitiensis* Meisn. (Lauraceae) (R.P.), *Dioscorea mummularia* Lam. (Dioscoreaceae) (R.P.), *Laportea vitiensis* Seem. (Urticaceae) (R.P.), leaves *Macaranga Seemanni* Mull-Arg. (Euphorbiaceae) (W.G.) and leaves *Artocarpus incisa* L. (Urticaceae) (W.G.).

Thysanoptera.

Liothrips urichi Karny. Feeds on *Clidemia hirta* Don. (Melastomaceae) (H.S.).—*Haplothrips gowdeyi* Frankl. Feeds on *Stachytarpheta jamaicensis* Vahl. (Verbenaceae) (H.S.).—*Microcephalothrips abdominalis* Crawf. Feeds in flower heads of *Vernonia cinerea* Less. (Compositae) (W.G.).

Anoplura.

Tarsonomidae: *Pediculoides ventricosus* Newp. Feeds on larvae of *Promecotheca reichei* Baly. (Hispidae) (T.T.).

Orthoptera.

Blattidae: *Eupella supellectilium* Son. Nymph and imago feed on books and papers (R.L.).

Isoptera.

The following white ants are recorded as damaging timber in Fiji: *Eutermes olidus* Hill (R.L.), *Coptotermes acinaciformis* Frogg. (R.L.), *Kalotermes repandus* Hill (R.L.), *K. buxtoni* Hill (R.L.), *K. taveuniensis* Hill (R.L.), *Prorhinotermes inopinatus* Silv. (R.L.).

Diptera.

The records for Diptera refer to the feeding habits of the larva unless otherwise stated.

Culicidae: *Aedes scutellaris* Walk. var. *horrescens* Edw. The female imago attacks human beings (R.P.).—*A. kochi* Don. Female imago attacks human beings (R.P.).—*Megarhinus splendens* Wied. Larvae predaceous on larvae of *Aedes variegatus* Dol. (Culicidae) (R.P.).

Trypetidae: *Dacus passiflorae* Frogg. Larvae feed in the following fruits: *Citrus aurantium* L. var. *japonica* (Rutaceae) (W.G.), *Inocarpus edulis* Forst. (Leguminosae) (H.S.), *Coffea liberica* Bull. (Rubiaceae) (H.S.), *Psidium Cattlei-*

anum Sabine (Myrtaceae) (H.S.), *Dracontomelon sylvestre* Bl. (Anacardiaceae) (H.S.), *Persea gratissima* Gaertn. (Lauraceae) (H.S.), *Capsicum grossum* (Solanaceae) (H.S.), *Chrysophyllum Cainito* L. (Sapotaceae) (H.P.), *Solanum Melongena* L. (Solanaceae) (H.P.), *Crescentia Cujete* L. (Bignoniaceae) (H.P.), *Tetranthera palmatinervia* Meisn. (Lauraceae) (W.G.), *Eugenia uniflora* L. (Myrtaceae) (W.G.), *E. braziliensis* Lam. (Myrtaceae) (R.L.), *Barringtonia speciosa* Forst. (Lecythidaceae) (H.S.), *Passiflora laurifolia* L. (Passifloraceae) (W.G.) and *Eugenia Jambos* L. (Myrtaceae) (W.G.).—*Dacus xanthodes* Broun. Larvae feed in the following fruits: *Passiflora quadrangularis* L. and *Carica Papaya* L. (Passifloraceae) (both H.S.).—*Ensina sororcula* Wied. Larvae feed in the flower heads of the following Compositae: *Coreopsis tinctoria* Nutt., *C. lanceolata* L., *Cosmos sulphureus* Cav., *Synedrella nodiflora* Gaertn. and *Tagetes patula* L. (all W.G.).—*Spheniscomyia binoculata* Bez. Larvae feed in the flowers of the following Labiatae: *Coleus Blumei* Benth. and *C. amboinicus* Lour. (both W.G.).

Ortalidae: *Pseudorichardia flavitarsis* Macq. Feed in ripe fruits of *Chrysophyllum Cainito* L. (Sapotaceae) (W.G.).

Muscidae: *Atherigona excisa* Thoms. var. *trilineata* Stein. Larvae feed in decaying trunks of *Musa sapientum* L. (Scitamineae) (W.G.).—*A. poecilopoda* Bez. In fruits of *Inocarpus edulis* Forst. (Leguminosae) (R.L.).

Syrphidae: *Xanthogramma javanum* Wied. var. *distinctum* Kertész. Larvae feed on all stages of *Neomaskellia bergii* Sign. (Aleurodidae) (R.V.).

Micropezidae: *Telostylinus lineolatus* Wied. Feeds in following fruits: *Crescentia Cujete* L. (Bignoniaceae) (H.P.) and *Inocarpus edulis* Forst. (Leguminosae) (R.L.).

Agromyzidae: *Melanagromyza alysicarpi* Bez. Larvae tunnel in leaves of *Uraria lagopoides* DC. (Leguminosae) (W.G.).—*Pseudonapomyza atra* Meig. Larvae mine in leaves of following Gramineae: *Eleusine indica* Gaertn. and *Cynodon Dactylon* Pers. (both W.G.).

Tachinidae: *Sturmia sericariae* Corn. Bred from larvae of the following Sphingidae: *Chromis erotus* Cram., *Hippotion celerio* L. and *Herse convolvuli* L. (all W.G.).—*Actia striglinae* Bez. Bred from larva of *Cirphis unipuncta* Haw. (Noctuidae) (W.G.).—*Ptychomyia remota* Ald. Parasitic on larvae of *Levuana iridescens* B-B. (Zygaenidae) (H.S. and T.T.).—*Erycia basifulva* Bez. Parasitic on *Tirathaba trichogramma* Meyr. (Pyralidae) (R.L.).—*Carcelia kockiana* Towns. Parasitic on *Cryptophlebia* (*Argyroploce*) *illepida* Butl. (Tortricidae) (R.L.).

TABULATION OF THE GENERA *AUSTROLIMNIUS* AND *NOTRIOLUS* [DRYOPIDAE] AND DESCRIPTION OF A NEW SPECIES OF *NYCTOZOILUS* [TENEBRIONIDAE].

By the late H. J. Carter, B.A., F.R.E.S.
(*Communicated by Dr. A. B. Walkom.*)

[Read 26th June, 1940.]

Table of Austrolimnius.

1.	Upper surface black	2
	Upper surface variegated or coloured	8
2.	Surface opaque	3
	Surface nitid	4
3.	Elytra granulose, size very small	(*Neosolus*) *tropicus* C. & Z.
	Elytra coarsely punctate	*montanus* King.
4.	Hind and/or mid tibiae dentate or enlarged	5
	All tibiae simple	7
5.	Metasternum carinate	*metasternalis* C. & Z.
	Metasternum non-carinate	6
6.	Mid tibiae dentate in middle, hind tibiae enlarged	*victoriensis* C. & Z.
	Mid tibiae dentate at apex, hind tibiae dentate at middle	*oblongus* C. & Z.
7.	Lateral margins of prothorax serrulate	*politus* King.
	Lateral margins of prothorax entire	*diemenensis* C. & Z.
8.	Elytra with four red spots	*luridus* C. & Z.
	Elytra without defined spots	9
9.	Margins of prothorax and elytral pattern red	*suffusus* C. & Z.
	Prothorax and elytra concolorous	10
10.	Head black, rest of surface opaque red, sculpture asperate	*atriceps* C. & Z.
	Whole surface yellow or brown, sculpture very fine	*variabilis* C. & Z.

Table of Notriolus.

1.	Oblong-ovate; disk of pronotum convex throughout	2
	More widely ovate; disk of pronotum in part flattened	14
2.	Upper surface concolorous	3
	Upper surface with pale markings	8
3.	Upper surface more or less nitid black, glabrous	4
	Upper surface setose, brown	*setosus* C. & Z.
4.	Upper surface very nitid	5
	Upper surface subnitid	6
5.	Prothorax widest behind middle, elytral striae clearly punctate	*barretti* C. & Z.
	Prothorax widest at middle, strial punctures almost hidden in deep striae	*simsoni* Grouv.
6.	Prothorax widest at base, elytral intervals strongly cross-wrinkled	*allynensis* C. & Z.
	Prothorax widest behind middle, intervals not as in *allynensis*	7
7.	Dimensions of *allynensis*, elytral intervals lightly strigose	*tropicus* C. & Z.
	Size smaller, elytral intervals sublaevigate	*minor* C. & Z.
8.	Elytra with 4 pale maculae	9
	Elytra with 2 humeral maculae only	13
9.	Surface opaque	*maculatus* Cart.
	Surface nitid	10
10.	Elytra subgibbous near base	11
	Elytra normally convex	*victoriae* C. & Z.
11.	Prothorax widest at middle	*quadriplagiatus* Cart.
	Prothorax widest behind middle	12

12. Underside black, prosternal process narrowed and rounded at apex .. *galstonius* C. & Z.
    Underside reddish-brown, process widely truncate at apex ..... *dorrigoensis* C. & Z.
13. Sides of prothorax evenly rounded, seriate punctures large ..... *davidsoni* C. & Z.
    Sides of prothorax strongly sinuate, seriate punctures small ..... *humeralis* C. & Z.
14. Elytra with 4 pale maculae ..... *taylori* C. & Z.
    Elytra black or with 2 humeral maculae 15
15. Surface in general black (rarely with humeral maculae) ..... *subplanatus* C. & Z.
    Elytra with apical margins and shoulder spot red ..... *minutus* C. & Z.

Nyctozoilus variabilis, n. sp.

Widely ovate and convex, subnitid black above, nitid black below.

Head: surface uneven, scarcely rugose, a transverse groove separating forehead from epistoma, a notch or depression at middle of base of forehead. *Antennae*: segment 3 as long as 4–5 combined, 8–10 transverse, 11 large and oval. *Prothorax*: apex strongly emarginate, anterior angles in ♂ lightly blunted, in ♀ widely rounded, sublobate; base truncate, sides well rounded, lightly sinuate in front and behind; post angles acute in ♂, subrectangular in ♀, foliate margins wide, subhorizontal, more or less wrinkled, extreme border scarcely raised; disk separated by light groove, irregularly rugose without defined medial sulcus, but with longitudinal depression on basal half. *Elytra* considerably wider than prothorax at base, widest behind middle, each with three, lightly raised and feebly undulate costae, the suture also raised; intervals irregularly punctate, with a few straggly, incomplete reticulations (more marked in ♀). *Prosternum* smooth, its process bisulcate; the rest of underside with shallow strioles, legs rather slender. *Dim.* 19 × 11 mm. (♀); 16–18 × 8–10 mm. (♂).

Hab.—Queensland: Tolmur (F. Cudmore).

Seven examples sent from the National Museum present one of those problems that occur in this group of the Tenebrionidae. Those I take to be ♂ (5 examples) are smaller, with front angles less rounded, but the general structure of thorax and the sculpture of elytra are so similar that I hesitate to separate them as species from the larger pair (♀). Holotype and allotype in National Museum, Melbourne. It belongs to the 1st group in my table (Proc. Linn. Soc. N.S.W., 1925, p. 235). The widely rounded front angles of ♀ are remarkable.

THE ECOLOGY OF THE CENTRAL COASTAL AREA OF NEW SOUTH WALES. III.

TYPES OF PRIMARY SUCCESSION.

By Ilma M. Pidgeon, M.Sc., Linnean Macleay Fellow of the Society in Botany.
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(Plates vi–viii; fourteen Text-figures.)

[Read 29th May, 1940.]

Introduction.

An analysis of the vegetation on the central coastlands of New South Wales type illustrates clearly that in any natural region the same climax is reached whether the succession begins in water, on rocks, or on wind-blown sand. A study of the mosaic of vegetation in this area reveals evidence of successions from xerarch and hydrarch conditions culminating in *Eucalyptus* Forest.

The purpose of this paper is to place on record a summary of the successions of vegetation of the central coastlands, and to discuss difficulties in the application of the concept of succession to this vegetation.

The concept of plant succession was proposed by Cowles (1901) to aid his classification of the vegetation around Chicago. He adduced for that district abundant evidence of physiographic development on sand dunes and rocks, in lakes, and in river valleys, and this development was accompanied by a succession of plants. Where there was a stable landscape, there was an apparently stable vegetation, the climax. The prime factor of the environment which determined the stage of succession reached in any habitat was water; habitats could be broadly defined as wetter or drier than the normal habitat which carried the climax.

This idea of succession was subsequently elaborated, burdened with a special nomenclature (Clements, 1916) and even endowed with philosophical significance (Phillips, 1935). It was applied to vegetation in other parts of the world, often with striking success (e.g. the work of Tansley and Watt), but on the Hawkesbury Sandstone in the central coastlands of New South Wales the difficulties in classifying vegetation are not totally overcome by using the principle of succession. In this paper, the opportunity is taken to discuss these difficulties and to put forward a few suggestions as to how they may be surmounted.

Types of Primary Succession.

The climate and physiography of the district have been described in earlier publications of this series (Pidgeon, 1937, 1938).

It is convenient to consider five different types of primary succession. The habitats available for colonization along these five developmental lines are:

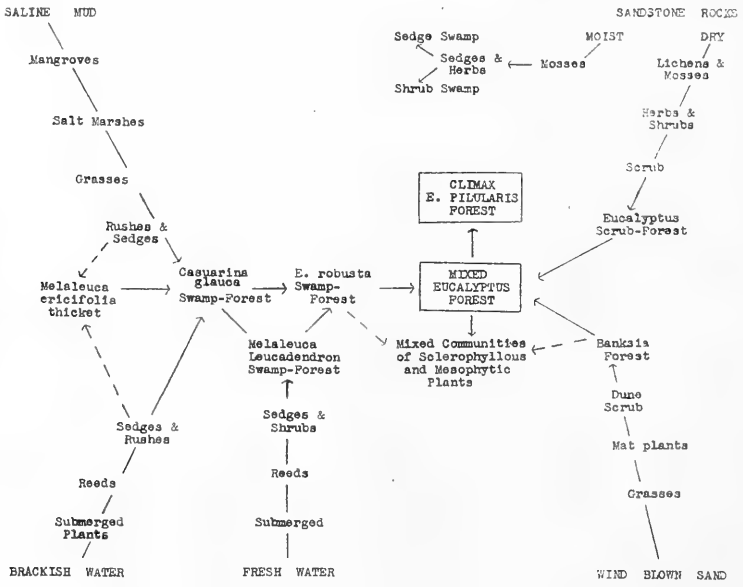
(i) Tidal mud flats.—Owing to the absence of delta-forming rivers, these are restricted to the arms and bays in the upper reaches of the estuaries which dissect the coastline. Saline flats are characterized by mangrove swamps.

(ii) Brackish water of numerous small lagoons and creeks.—These occur on the coastal plains, particularly north of Sydney. A series of zoned swamp-communities are found on the margins of these areas.

(iii) Fresh water of inland creeks or rivers, or, less frequently, of extensive drainage basins in stabilized wind-blown sands.—Owing to their limited extent, freshwater swamps are not of much importance.

(iv) Dunes and wind-blown sand of the beaches.—Since the coastline consists of alternating headlands and beaches, dunes form an extensive series.

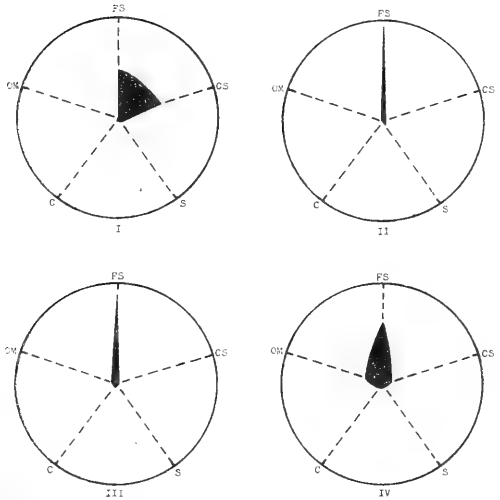
(v) Hawkesbury Sandstone rock.—With the exception of the Sydney Plains and a narrow coastal plain, the central coastlands consist of a sandstone plateau; consequently this lithosere is the most important of the successions in this area. The forests developed on sandstone have been referred to in earlier publications of this series as the Mixed *Eucalyptus* Forest Association.



Text-fig. 1.—Diagrammatic representation of plant successions in the central coastlands and their convergence to Mixed *Eucalyptus* Forest. (N.B.—Freshwater river succession omitted.)

There are lithoseres other than that occurring on sandstone, e.g. on shales which form the coastal plains and isolated cappings on the sandstone plateau. However it is practically impossible to trace these successions since the shales are all partially weathered and mostly covered by mature forests. The most important of these forests is the *E. saligna–E. pilularis* Association.

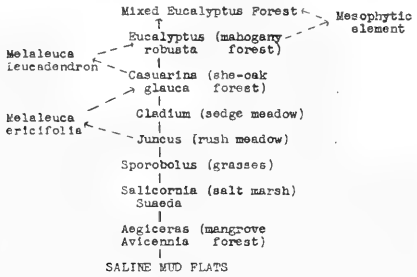
As previously stated, there is evidence of a general succession from xerarch and hydrarch conditions to Mixed *Eucalyptus* Forest (Text-fig. 1). A diagrammatic representation of the mechanical analysis of the substrates on which the successions are initiated is given in Text-figure 2.



Text-fig. 2.—Diagrammatic representation of the mechanical analysis of the four substrates on which succession is initiated: I, Hawkesbury Sandstone rock; II, Wind-blown sand; III, Salt swamp; IV, Brackish swamp. The material for I was obtained by lightly grinding a piece of rock in water. The percentage coarse sand (CS), fine sand (FS), silt (S), clay (C), and organic matter (OM) are plotted along the 5 axes of the circle, the radii of which represent 100%.

The different seres are discussed in the following sections.

(i) *Succession on Saline Mud Flats.*



Text-fig. 3.—Diagrammatic representation of succession on saline mud flats.

(*a*) *Zonation.*

In the succession* initiated on the mud flats of estuaries open to tidal scour, mangroves are the first colonists to become established under the extreme conditions of moisture, aeration and salinity. The mangroves are bounded on the landward margin by a series of zoned communities of saltmarsh plants, grasses, rushes, sedges, and trees (Pl. vii, figs. 1, 2). This sequence is outlined in Text-figure 3.

* This is the first complete account of succession in mangrove swamps in N.S.W. Hamilton (1919) and Collins (1921) have recorded, in the Sydney district, the succession up to the *Casuarina* stage. Hamilton's paper is chiefly floristic; the zones recognized by him are: 1, The Tide-flooded Zone (Mangroves and *Salicornia*); 2, The Dry Salt Plain; 3, The Fluvial Zone (*Casuarina*). Collins' zonation is as follows: A, Mangrove Formation; B, Saltmarsh Formation—(i) Salicornietum, (*a*) *Salicornia-Suaeda* Associes, (*b*) *Salicornia-Spergularia* Associes, (*c*) *Sporobolus-Cynodon* Associes; (ii) Juncetum.

As soon as mudbanks are raised above low-tide level, mangroves become established. It is noteworthy that *Salicornia* is not the pioneer on salt marshes, as in Europe, but succeeds the mangrove swamp.

There are two mangroves, *Aegiceras majus*, a shrub about 2 metres in height, and *Avicennia officinalis*, a tree from 5 to 9 metres. *Aegiceras* has the greater range; it occurs further out into the estuary, sometimes almost covered by high tide, and extends further inland. *Aegiceras* can also tolerate a higher percentage of fresh water. *Avicennia* typically occurs as a ribbon community between the zones of *Aegiceras*. The drainage channels which dissect the saltmarsh are frequently outlined by *Aegiceras* and a dwarfed form of *Avicennia* (Pl. vii, fig. 1).

Assisted by *Zostera*, the mangroves catch debris and silt and so build up and consolidate the mud. The genera of algae which have been recorded at this stage in the succession include *Cladophora*, *Ulva* and *Enteromorpha*. Saltmarsh plants, the first of which are *Salicornia australis*, *Suaeda australis* and *Samolus repens*, invade the landward margin of the mangrove area. With subsequent silt accumulation the mangroves are forced further out into the estuary and in their place a saltmarsh is formed. The extension of the mangrove forest into the estuary is limited by the depth of the tidal waters. In the saltmarsh, *Salicornia* is the dominant and frequently occurs as an almost continuous carpet (Pl. vii, figs. 1, 2.). Species other than those previously mentioned, which occasionally assume local dominance, are *Triglochin striata* and *Spergularia rubra*. On the landward margin of the saltmarsh, beyond the influence of tides, *Sporobolus virginicus* forms a dense sward in which scattered tufts of other grasses become established. The next invader is the rush *Juncus maritimus* which forms a dense stand in which *Sporobolus* frequently occurs as a sub-dominant. *Juncus* is succeeded on the landward margin by *Cladium junceum*; both species form ribbon communities which intermingle at their junction. The sedge is followed by the swamp she-oak, *Casuarina glauca*. At this stage the soil is still saline (Text-fig. 4) and has a high water-content. Under conditions of fresh, or almost fresh, water drainage, the *Casuarina* forest is replaced by *Eucalyptus robusta*. When the soil is sufficiently well drained, other trees such as *Eucalyptus botryoides*, *E. umbra*, *E. punctata*, etc. (see Table i), invade the area. All these species are not present in the one stand. These Eucalypts are also typical of sandstone soils; they are the first representatives of the Mixed *Eucalyptus* Forest Association, the "climax" of the various types of succession in this area.

Evidence that these swamps represent a dynamic succession and not a static zonation is obtained by the occurrence of relict species in more advanced zones, and also by the invasion of species such as *Juncus* into the *Salicornia* meadow. Doubt has often been expressed that succession progresses beyond the *E. robusta* stage, because in most sites of colonization in the Sydney district the swamp forest merges almost immediately into the sandstone slope of the foreshore. However, unquestionable evidence of succession has been obtained from the colonization of a mud island in the Port Stephens estuary. This island is outlined by mangroves which are succeeded by concentric zones of the various stages culminating in a nucleus of *E. robusta* and *Angophora lanceolata*, and subtropical rain-forest trees such as *Livistona australis* and *Ficus stenocarpa*.

A few variations occur in the sequence of the stages outlined above. These are:

(i) A thicket of *Melaleuca ericifolia* sometimes occurs between the *Juncus* or *Cladium* and *Casuarina* zones. The factors governing the occurrence of this species in the sere are not known.

(ii) The paper-bark tea-tree, *Melaleuca Leucadendron*, usually forms a definite stage between the *Casuarina* and *E. robusta* forests in the northern part of the area (Pl. viii, fig. 1). This species is at its southern limit in the vicinity of Gosford.

(iii) In sheltered areas a mixture of mesophytic or marginal rain-forest species may occur in the *E. robusta* forest (see Table i).

The extent of the swamp varies according to the nature of the shoreline and the amount of silt deposited. All the stages of the sere may be present in horizontal zonation, but there are no really extensive tidal flats. In most cases some of the zones are absent or telescoped, and in extreme cases where rocky foreshores rise steeply from deep water, the sere is reduced to a band of mangroves with a single line of *Casuarina* marking the junction of foreshore and mud.

Table i includes the typical species in each stage of the sere.

TABLE i.

Species List of the Stages of Mangrove Swamp Succession.

Stage of Succession.	Dominants.	Sub-dominants.
Mangrove forest	*Aegiceras majus* Gaertn.	
	Avicennia officinalis Linn.	
Salt Marsh	*Salicornia australis* Soland.	
	Suaeda australis R.Br.	
	Triglochin striata Ruiz. and Pav.	
	Spergularia rubra Camb.	
	Wilsonia Backhousii Hook.	
Perennial carpet-formers.	*Samolus repens* Pers.	
	Mesembryanthemum tegens F.Muell.	
	Cotula coronopifolia L.	
	C. reptans Benth.	
	Selliera radicans Cav.	
	Lobelia anceps Thunb.	
Annuals scattered through marsh.	*Tetragonia expansa* Murr.	
	Atriplex patula L.	
Grass Meadow	*Sporobolus virginicus* Humb. and Kunth.	
	Zoisia macrantha Desv.	
	Cynodon Dactylon Rich.	
Annuals occurring as scattered tufts.	*Agrostis aemula* R.Br.	
	A. Billardieri R.Br.	
	Lepturus incurvatus Trin.	
Rush Meadow	*Juncus maritimus* Lam.	*Sporobolus*, etc.
Sedge Meadow	*Cladium junceum* R.Br.	
Tea-tree thicket	*Melaleuca ericifolia* Sm.	
She-Oak Forest	*Casuarina glauca* Sieb. (with epiphytic *Dendrobium teretifolium* R.Br.)	*Melaleuca linariifolia* Sm.; *M. styphelioides* Sm.; *Cladium junceum* R.Br.; *Juncus maritimus* Lam.; *Schoenus brevifolius* R.Br.; *Leptocarpus tenax* R.Br.; *Gahnia psittacorum* Labill.
Paper-bark Tea-tree Forest	*Melaleuca Leucadendron* Linn.	*Selaginella uliginosa* Spring.; *Hydrocotyle tripartita* R.Br.; *Ranunculus parviflorus* Linn.; *Scirpus inundatus* Spreng.; *S. riparius* Spreng. (ground flora.); *Lyonsia reticulata* F.v.M. (Creeper)

TABLE i.—*Continued.*

Species List of the Stages of Mangrove Swamp Succession.—Continued.

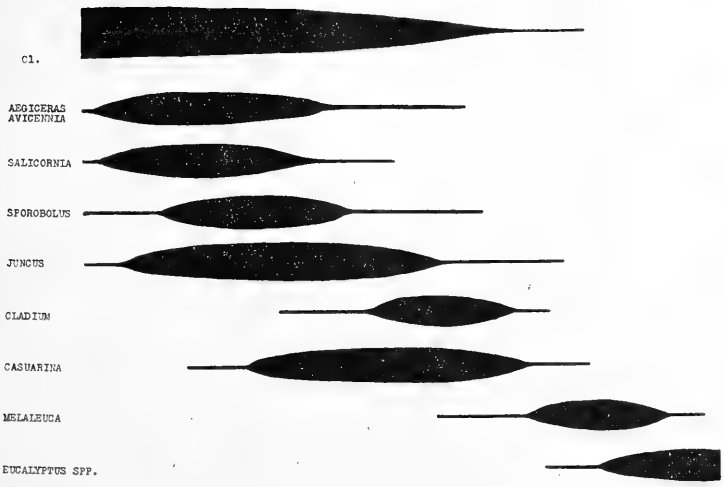
Stage of Succession.	Dominants.	Sub-dominants.
Swamp-mahogany Forest	*Eucalyptus robusta* Sm.*	*Gahnia psittacorum* Labill. *Restio tetraphyllus* Labill. *Pteridium aquilinum* L. *Blechnum serrulatum* Rich. *Pellaea falcata* (R.Br.) Fee. *Cyperus polystachyus* Rottb. *Viola hederacea* Labill. *Goodenia ovata* Sm.
Mesophytic element (in *E. robusta* Forest)	*Eugenia Smithii* Poir. *Livistona australis* Mart. *Backhousia myrtifolia* Hook. and Harv. *Endiandra Sieberi* Nees. *Pittosporum revolutum* Ait. *Ficus stenocarpa* F.v.M. *Cupaniopsis anacardioides* Radlk. *Myoporum tenuifolium* Forst. *Elaeocarpus oboratus* G.Don. *Acronychia laevis* Forst. *Citriobatus multiflorus* Cunn.	Creepers *Sarcopetalum Harveyanum* F.v.M. *Tecoma australis* R.Br. *Geitonoplesium cymosum* Cunn. *Vitis clematidea* F.v.M. *Hibbertia volubilis* Andr. *Lyonsia* spp.
Mixed *Eucalyptus* Forest	*Angophora lanceolata* Cav. *Eucalyptus botryoides* Sm. *E. umbra* R.T. Baker. *E. punctata* DC. *E. paniculata* Sm. *E. eugenioides* Sieb. *E. resinifera* Sm. *E. pilularis* Sm.	Various scierophyllous undershrubs.

* In the northern districts this species may be accompanied by *E. Kirtoniana* F.v.M.

(*b*) *Changes in the Environment.*

Salt swamp soils are typically grey and, although the mechanical composition varies according to the nature of the depositing current, distance transported, and type of parent rock, in this district they are usually of a sandy texture since they are derived mainly from the surrounding sandstone country (see Text-fig. 2). Detailed mechanical analyses of soil were not carried out, but from the work done it was evident that there is an increase in the humus content in the later stages of the sere.

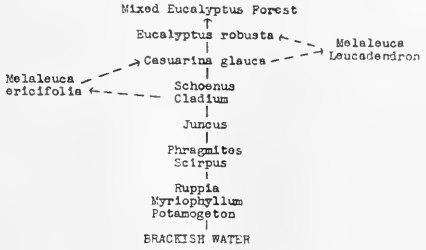
The salt content of mangrove-swamp soils is the only environmental factor which has been studied in any detail. The results are presented graphically in Text-figure 4. The chloride content from the mangrove to the *Juncus* zones is very variable and depends on the conditions at the time of sampling, e.g. estimations made during a drought period following high spring-tides show the greatest concentrations in the *Salicornia* or *Juncus* zones rather than in the mangrove zone. It appears that the chloride content falls progressively through the *Sporobolus* and *Juncus* meadow, and is markedly decreased in the *Cladium* zone. It is still high in the *Casuarina* forest, but falls off gradually towards the *Melaleuca Leucadendron* zone, until in the *Eucalyptus* forest the drainage is practically fresh.



Text-fig. 4.—Relation between salt concentration of soil (as Cl) and distribution of dominants in seral stages of salt marsh succession.

The mangroves are restricted to the area between high tide and low tide. Tide plays an important part in the development of English salt-marshes (Chapman, 1939), and it is probable that this factor limits the *Salicornia* meadow here. The extent of the various zones may be said to be limited by environment towards the hydrarch end of the sere, and by competition at the mesarch end. The succession from *Eucalyptus robusta* to Mixed *Eucalyptus* Forest depends to a large extent on allogenic factors.

(ii) *Brackish-water Succession.*



Text-fig. 5.—Diagrammatic representation of succession in brackish water.

The coastal lagoons are only open to the sea intermittently and may be closed during periods of several years. The chloride percentage therefore varies considerably, but the water is never fresh.

Succession around these brackish lagoons differs from the previous sere in that submerged plants and reeds occur instead of the mangroves and salt-marshes (Pl. vi, fig. 4). There is also a greater variety of sedges than in the salt-water succession, but otherwise the seral stages are similar (Text-fig. 5).

On the margins of a few rivers, it has been possible to trace the gradual transition from salt to brackish water succession. *Phragmites* and *Aegiceras* are

intermingled in the first zone, but *Avicennia* is absent, and the second zone consists of *Juncus* and *Cladium* instead of salt marshes.

Most of the brackish-water successions have been partially destroyed, especially in the Sydney district. The most extensive examples occur in the Myall Lakes (Osborn and Robertson, 1939). In most cases, very little Mixed *Eucalyptus* Forest is ever developed; the *Casuarina* forest frequently abuts on *Eucalyptus* forest developed on soil weathered in situ from sandstone, or else it merges into hind-dune forest, because the lagoons usually occur at the rear of the beaches. On the south coastal plain, the brackish lakes and creeks are not surrounded by sandstone country, but by alluvial deposits, mudstones, shales, etc.; consequently the climax forest consists of any of the following species: *Eucalyptus eugenioides, E. longifolia, E. saligna, E. pilularis, E. amplifolia, E. paniculata, Angophora intermedia, Melaleuca linariifolia.* The most outstanding environmental change, as in any hydrosere, is reclamation by the building up of a soil and consequent lowering of the water-table. By contrast with the soil changes in mangrove succession, there is a decrease in percentage humus in the climax stage (cf. diagrams iii and iv, Text-fig. 2).

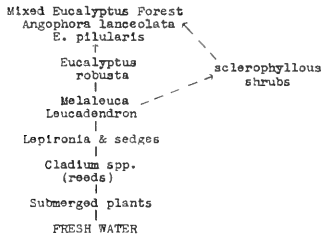
Table ii contains a list of the species typical of the early phases of the sere.

TABLE ii.

Typical Species of the Early Stages of Brackish-water Succession.

Stage of Succession.	Dominants.	Sub-dominants.
Submerged plants.. ..	*Ruppia maritima* L.	
	Myriophyllum sp.	
	Potamogeton spp.	
	Cladophora sp.	
	Chara sp.	
	Nitella sp.	
Amphibious reeds ..	*Scirpus lacustris* L.	
	S. littoralis Schrad.	
	Phragmites communis Trin.	
	Triglochin procera R.Br.	
Emerged rushes and sedges	*Juncus maritimus* Lam.	*Selliera radicans* Cav.
	Cladium junceum R.Br.	*Cotula coronopifolia* L.
	Schoenus brevifolius R.Br.	*C. reptans* Benth.
	Leptocarpus tenax R.Br.	*Apium prostratum* Labill.
		Hydrocotyle vulgaris L.
		H. Asiatica Linn.
		Samolus repens Pers.
		Scirpus riparius Spreng.
		S. carnuus Vahl.
		Lobelia anceps Thunb.
		Mimulus repens R.Br.
		Viola hederacea Labill.
		Sclaginella uliginosa Spring.
		Stackhousia viminea Sm.

(iii) *Freshwater Succession.*



Text-fig. 6.—Diagrammatic representation of freshwater swamp succession in wind-blown sands.

(a) Swamps in Sands.

Series of extensive freshwater swamps occur in the Port Stephens* district in undulating areas of stabilized wind-blown sands. It is probable that these swamps have originated as drainage basins caused by the cupping of the underlying rocks. The soil in these swamps consists of black silt mixed with sand; it has approximately the same composition as that of brackish swamps.

The stages of the sere are shown in Text-figure 6. The climax is the same as that occurring on the adjacent wind-blown sands. Several swamps showed complete sequences from free water to *Eucalyptus* forest, which merged gradually into the forest on wind-blown sand (Pl. vii, fig. 3). Various stages in the reclamation of the swamps were found, e.g. in one place there was observed a swamp almost dried out, consisting of a glade of *Melaleuca Leucadendron* and *Eucalyptus robusta.* Fires are prevalent in this area, and, if severe, they appear to divert the swamp temporarily in its later stages to a shrub or heath community reminiscent of shrub swamps on Hawkesbury Sandstone (see p. 238). Evidence for this is in the occurrence of partially dead or burned clumps of *Melaleuca* in a community of moisture-tolerant herbs and shrubs (see Table iii), together with relict species such as *Restio, Schoenus, Leptocarpus,* etc., from the *Melaleuca* zone. Swamps in this state, however, eventually develop into a typical climax of *Angophora lanceolata* and *E. pilularis,* indicated by marginal invasion of seedlings of these species. Table iii is a list of the species of frequent occurrence in the Port Stephens swamps (N.B.—submerged stage not listed). An inspection of Table iii shows that the outstanding point of difference of this sere from brackish succession is that *Juncus maritimus* and *Casuarina glauca* are absent.

Similar swamps of lesser extent occur in the sands at Botany Bay, Maroubra and La Perouse (Sydney), but they are much disturbed, and in a few years will have been completely reclaimed by man.

* This is actually north of the area defined in Part (i) as central coastlands.

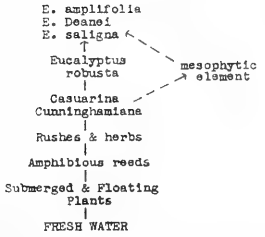
TABLE iii.

Typical Species of Freshwater Swamps in Wind-blown Sands at Port Stephens.

Stage of Succession.	Dominants.	Sub-dominants.
Amphibious reeds ..	*Cladium teretifolium* R.Br. *C. articulatum* R.Br. *Triglochin* spp. *Philydrum lanuginosum* Banks. **Lepironia mucronata* Rich.	
Emerged stage ..	*Lepironia mucronata* Rich. **Melaleuca Leucadendron* L. (seedlings)	*Scirpus inundatus* Spreng. *Gratiola pedunculata* R.Br. *Drosera spathulata* Labill. *Villarsia reniformis* R.Br.
Tea-tree forest ..	**Melaleuca Leucadendron* L.	*Cladium junceum* R.Br. *Schoenus brevifolius* R.Br. *Restio australis* R.Br. *Leptocarpus tenax* R.Br. *Restio tetraphyllus* Labill. *Sprengelia incarnata* Sm. *Boronia parviflora* Sm. *Epacris obtusifolia* Sm. *Halorrhagis micrantha* R.Br.
Eucalyptus and Tea-tree forest.	**Melaleuca Leucadendron* L. *E. robusta* Sm.	*Blechnum serrulatum* Rich. *Restio tetraphyllus* Labill. *Villarsia reniformis* R.Br. *Halorrhagis micrantha* R.Br. *Hydrocotyle tripartita* R.Br. *Sphagnum* sp. *Viola hederacea* Labill.
Climax— Mixed Eucalyptus forest	*E. pilularis* Sm. *Angophora lanceolata* Cav.	Sclerophyllous shrubs.
	Shrubs.	Herbs.
Moisture-tolerant herbs and shrubs from "heath" community (in addition to species listed as sub-dominant strata in Tea-tree forest).	*Callistemon lanceolatus* DC. **Melaleuca thymifolia* Sm. *M. genistifolia* Sm. *Hakea pugioniformis* Cav. *H. dactyloides* Cav. *Leptospermum juniperinum* **L. Liversidgei* R. T. Baker *Viminaria denudata* Sm. *Olax stricta* R.Br. *Banksia latifolia* var. *minor* Maiden and Camfield *Dillwynia floribunda* Sm. **Boronia falcifolia* Cunn. **Sprengelia Ponceletia* F.v.M. *Baeckea diffusa* Sieb.	*Burchardia umbellata* R.Br. *Sowerbaea juncea* Sm. *Xyris gracilis* R.Br. *Restio gracilis* R.Br. *Mitrasacme polymorpha* R.Br. *Selaginella uliginosa* Spring. *Lepyrodia scariosa* R.Br. *Dampiera stricta* R.Br. *Lepidosperma laterale* R.Br. *Goodenia stelligera* R.Br. *Euphrasia Brownii* F.v.M.

* These species are not typical of the Sydney District.

(*b*) *River Succession.*



Text-fig. 7.—Diagrammatic representation of marginal freshwater river succession.

Most of the coastal rivers are in a youthful stage of development and flow through deep gorges, so space for marginal succession is limited. When the sere is present it is always foreshortened and is frequently limited to the reed and *Casuarina* stages. The headwaters of creeks often lose themselves in small swamps, which consist floristically of representatives from the initial stages only. Succession is frequently not progressive in these situations, not only because of the sharp rise to the surrounding slopes, but because the latter are a continuous source of drainage water.

This succession is represented diagrammatically in Text-figure 7, and the most frequent species in each stage are listed in Table iv. The absence of *Melaleuca Leucadendron* from this sere is notable; this species grows only in stagnant water. The principal differences between river successions in fresh and brackish water are that in fresh water *Casuarina Cunninghamiana* replaces *C. glauca*, and *Juncus pauciflorus* and others replace *J. maritimus*.

The climax of *Eucalyptus* species growing on silty banks is usually a pure stand of *E. saligna*, *E. Deanei* or *E. amplifolia*. Since the soils in these habitats consist mainly of fine river alluvium, *Eucalyptus* species typical of heavier soils occur rather than representatives of the Mixed *Eucalyptus* Association, which are practically restricted to light sandy soils. In addition, if the climax of this sere is developed in Hawkesbury Sandstone country, the creek has usually cut its base level to the softer strata of the Narrabeen Series; alternatively, as at Cattai Creek, the surrounding country is of Wianamatta Shale, so clay and silt particles rather than sand are washed on to the river alluvium. This accretion of clay and silt is in contrast to most other hydroseres in the central coast in which the development of Mixed *Eucalyptus* Forest is partly determined by the downwash of sand from the surrounding sandstone slopes.

At Cattai Creek (Windsor) a fairly complete sere is present, although telescoping occurs in the initial stages. However, in the *Casuarina–E. robusta* forest there is a good representation of mesophytic species including *Ficus aspera*, *Eugenia Smithii*, *Cryptocarya* sp., *Claoxylon australe*, *Lyonsia reticulata* and *Stephania hernandifolia*.

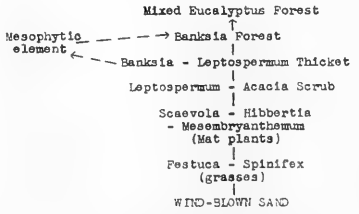
TABLE iv.

Typical Species of Freshwater River Succession.

Stage of Succession.	Dominants.	Sub-dominants.
Submerged or floating..	*Utricularia* spp.	
	Vallisneria spp.	
	Potamogeton spp.	
	Cabomba peltata F.v.M.	
	Najas marina L.	
	Myriophyllum spp.	
Amphibious reeds ..	*Phragmites communis* Trin.	
	Eleocharis spp.	
	Typha angustifolia Linn.	
	Triglochin spp.	
	Philydrum lanuginosum Banks.	
Emerged* rushes and herbs.	*Juncus pauciflorus* R.Br.	*Carex* spp.
	J. pallidus R.Br.	*Scirpus prolifer* Rottb.
	J. planifolius R.Br.	*Villarsia reniformis* R.Br.
	Agrostis avenacea Gmel.	*Alisma plantago* L.
	Gahnia spp.	*Ranunculus rivularis* Bks. & Solander
		Gratiola Peruviana Linn.
She-oak forest	*Casuarina Cunninghamiana* Miq.	*Goodenia paniculata* Sm.
	(+*Melaleuca linariifolia* Sm.	*Hydrocotyle hirta* R.Br.
	M. styphelioides Sm.	*H. asiatica* Linn.
	Callistemon salignus DC.)	*Viola hederacea* Labill.
		Prunella vulgaris Linn.
		Stellaria flaccida Hook.
		Schoenus apogon Roem. & Schult.
Eucalyptus forest ..	*E. robusta* Sm.†	*Oplismenus setarius* Roem. & Schult.
		Blechnum serrulatum Rich.
		Adiantum sp., etc.
Climax	*E. amplifolia* Naudin.	
	E. Deanei Maiden.	
	E. saligna Sm.	

* Ground flora subject to partial submergence.
† Restricted to coastal plain.

(iii) *Succession on Sand Dunes.*



Text-fig. 8.—Diagrammatic representation of succession on sand dunes.

(a) Zonation.

As in the hydrarch successions, the stages of sand-dune succession* are arranged spatially in horizontal zonation. The frequent "blow-outs" on the dunes often reveal old soil horizons which indicate the vertical sequence in time.

* Dune flora in the vicinity of Sydney was first recorded by Hamilton (1918); the first published account of succession on sand dunes in N.S.W. is by Osborn and Robertson (1939), who described the sere in the Myall Lakes District. The above account is a summary of sand-dune succession throughout the central coastlands.

Succession on wind-blown sand begins, as all over the world, with sand-binding and hummock-building grasses. These are succeeded by deep-rooting, creeping and trailing plants which bind the sand and form mats of vegetation. With sand stabilization woody shrubs appear and eventually form a dense dune scrub, while the sand-binding species disappear. In the absence of fires or other interference, the scrub thickets are replaced by *Banksia* forest and finally by Mixed *Eucalyptus* Forest. This sequence is summarized in Text-figure 8.

A number of strand plants such as the cosmopolitan sea-rocket, *Cakile maritima*, occur as scattered individuals, but play no part in succession.

There are two pioneer grasses of the unstable dune sand: *Festuca littoralis* and *Spinifex hirsutus*. *Festuca* grows in tussocks and collects hummocks of sand. *Spinifex* has long branched rhizomes which give off shoots and deeply descending roots at the nodes; it is thus a very effective sand binder (Pl. vi, fig. 3). Scattered individuals or colonies of the low growing *Senecio* spp. and *Sonchus* spp. usually occur with the grasses. Occasionally *Senecio spathulatus* forms an extensive series of miniature dunes above the strand (Pl. vi, fig. 1).

The mat-forming succulents, *Hibbertia volubilis*, *Scaevola suaveolens* and *Mesembryanthemum aequilaterale*, play an important part in sand stabilization. They form extensive and dense carpets and their deep roots hold the sand so firmly that, like *Festuca*, they often remain as hummocks after wind has partially destroyed the dune on which they were growing. A number of other plants are associated in the same zone with these succulents (see Table v). Most of them have a creeping habit, e.g. *Euphorbia* and *Pelargonium*, others are densely tufted rhizomatous types, e.g. *Lomandra* and *Scirpus* (Pl. vi, fig. 2).

On most of the beaches *Festuca* and *Spinifex* occupy a low unstable foredune which is usually discontinuous. Between this and the foreshore there may also be small hummocks of *Festuca* and trailing stems of *Spinifex* (Pl. vi, fig. 2). The mat plants usually occur as low mounds or high residual hummocks between the foredune and the first stable dune, often ascending the dune face, whereas the grasses rarely extend beyond the second zone. Woody shrubs, which form the third zone, usually occupy part or all of the windward face and crest of the first line of fixed dunes. The pioneer shrubs are *Correa alba*, *Leucopogon Richei*, *Leptospermum laevigatum* and *Acacia Sophorae*. Other shrub species are listed in Table v. Plants of the second zone, especially *Lomandra*, *Scirpus* and *Euphorbia*, mingle with the foremost shrubs. On dunes undisturbed by fire or wind storms the shrubs usually form a dense closed community pruned to a definite height according to the severity of the exposure. Towards the crest of the dune the scrub is typically composed of a few species only, usually *Leptospermum*, *Acacia*, *Leucopogon* and *Banksia*, which form a dense shrubbery about 2 metres in height. Immediately over the dune crest the height of the shrubs increases considerably; the lee slope is covered by closed thickets of *Leptospermum laevigatum* and *Banksia* spp., chiefly *B. integrifolia*. Mesophytic creepers and small trees (see Table v) take advantage of the increased shelter and humidity afforded by the lee slope and intermingle in the thickets. This temporary mesophytic element is a characteristic feature of the dune flora and is represented either by scattered individuals or local communities. Owing to the density of the thickets, there is little ground flora.

As the lee slope flattens out, the Banksias assume dominance and the closed thickets are replaced by open *Banksia* woodland (Pl. vii, fig. 4). The climax on stabilized dunes or inter-dune flats is *Eucalyptus* forest. That this stage succeeds

the *Banksia* woodland is indicated by the occurrence of *Banksia* spp. as a discontinuous second stratum in parts of the *Eucalyptus* forest. A certain amount of shelter is necessary before woodland or forest is established, so the first line of dunes on the ocean front rarely progresses beyond the impenetrable thicket stage. However, on high dunes developed in the shelter of a bay or inlet, climax forest has been recorded as extending almost to the limit of the strand.

Banksia serrata and *B. aemula* are the most typical species in the woodland and they often occur as pure communities, although *Angophora lanceolata* is a frequent associate. The woodland averages about 8 metres in height, and in sheltered dune hollows the undergrowth is characterized by *Pteridium aquilinum*, a few Cyperaceous species, herbs such as *Pomax umbellata*, and a number of creepers. In undulating areas open to the sun the Banksias are not so closely spaced and a variety of sclerophyllous shrubs form a dense stratum. There are several species of *Eucalyptus* which can succeed the Banksias, but they are all species which occur also in sandstone forests. In the south of the central coastlands *E. botryoides* is a typical dominant in the hind dune forest, but gradually diminishes in importance to the north and reaches its northern limit at Port Stephens. In the northern section *E. pilularis* frequently forms pure stands on well-drained sites, although this species is not so well developed as in sandstone gullies. *E. gummifera*, *Angophora lanceolata*, *A. intermedia* and *E. micrantha* occur also on stabilized dunes. The undergrowth in the *Eucalyptus* forests on stabilized dunes consists chiefly of sclerophyllous shrubs, some of which are recorded in Table v.

TABLE v.

Species List of Plant Indicators on Sand-dunes.

Stage of Succession.	
Zone 1.	
(*a*) Strand plant	*Cakile maritima* Scop.
(*b*) Grasses and associated herbs	*Spinifex hirsutus* Labill.
	Festuca littoralis Labill.
	Senecio lautus Sol.
	S. spathulatus A. Rich.
	Sonchus asper Hill.
	S. maritimus Linn.
Zone 2.	
(*a*) Mat plants	*Scaevola suaveolens* R.Br.
	Hibbertia volubilis Andr.
	Mesembryanthemum aequilaterale Haw.
(*b*) Minor mat-forming or creeping plants	*Stephania hernandifolia* Walp.
	Convolvulus Soldanella L.
	Pelargonium australe Willd.
	Apium prostratum Labill.
	Euphorbia Sparmannii Boiss.
	Stackhousia spathulata Sieb.
	Hydrocotyle vulgaris L.
	Cynodon dactylon Rich.
(*c*) Tufted plants	*Lomandra longifolia* Labill.
	Scirpus nodosus Rottb.
	Dianella coerulea Sims.
	Cynodon dactylon Rich.
	Carex pumila Thunb.
Zone 3.	
Shrubs	*Leptospermum laevigatum* F.v.M.
	Acacia Sophorae R.Br.
	Myoporum ellipticum R.Br.
	Leucopogon Richei R.Br.
	Correa alba Andr.
	Banksia integrifolia Linn.
	Monotoca scoparia R.Br.

TABLE V.—*Continued.*

Species List of Plant Indicators on Sand-dunes.—Continued.

Zone 4.	
(*a*) *Leptospermum-Banksia* thicket	*Leptospermum laevigatum* F.v.M.
	Banksia integrifolia Linn.
	B. serrata Linn.
(*b*) Mesophytic element. (Shrubs or small trees).	*Cupaniopsis anacardioides* Radlk.
	Notelaea longifolia Vent.
	Eugenia Smithii Poir.
	Myrsine variabilis R.Br.
	Wickstroemia indica C. A. Mey
	Stephania hernandifolia Walp. (creeper)
	Breynia oblongifolia J.Muell.
Zone 5.	
Banksia Forest	*Banksia serrata* Linn.
	B. aemula R.Br.
	B. integrifolia Linn.
Zone 6.	
Eucalyptus Forest	*Eucalyptus pilularis* Sm.
	E. botryoides Sm.
	Angophora lanceolata Cav.
	A. intermedia DC.
	E. gummifera (Gaertn.) Hochr.
	E. micrantha DC.
Sub-dominant strata of Zones 5 and 6.	
(i) In sheltered hollows (shrubs, herbs and creepers)	*Ricinocarpus pinifolius* Desf. } Shrubs
	Pimelia linifolia Sm. } Shrubs
	Monotoca scoparia R.Br. } Shrubs
	Correa speciosa Andr. } Shrubs
	Pteridium aquilinum L.
	Lomandra longifolia Labill.
	Imperata cylindrica var. *Koenigii* Durand & Schinz.
	Xanthosia pilosa Rudge
	Pomax umbellata Sol.
	Halorrhagis teucrioides A. Gray
	Kennedya rubicunda Vent. } Creepers
	Hibbertia volubilis Andr. } Creepers
	Smilax glycyphylla Sm. } Creepers
(ii) In open undulating areas (sclerophyllous shrubs)	*Leucopogon ericoides* R.Br.
	L. virgatus R.Br.
	Zieria laevigata Sm.
	Eriostemon lanceolatus Gaertn.
	Bossiaea ensata Sieb.
	Calycothrix tetragona Labill.
	Styphelia viridis Andr.
	Chloanthes Stoechadis R.Br.
	Persoonia lanceolata Andr.
	Acacia suaveolens Willd.
	Dillwynia ericifolia Sm.
	Aotus villosa Sm.
	Ricinocarpus pinifolius Desf.
	Conospermum spp.
	Lepidosperma laterale R.Br.
	Tetratheca ericifolia Sm.

In seepage areas in dune hollows local swamp communities sometimes occur, but are not a marked feature of the dune flora. Species typical of these habitats are *Melaleuca ericifolia, M. linariifolia, Gahnia psittacorum, Restio tetraphyllus* and *Scirpus nodosus.*

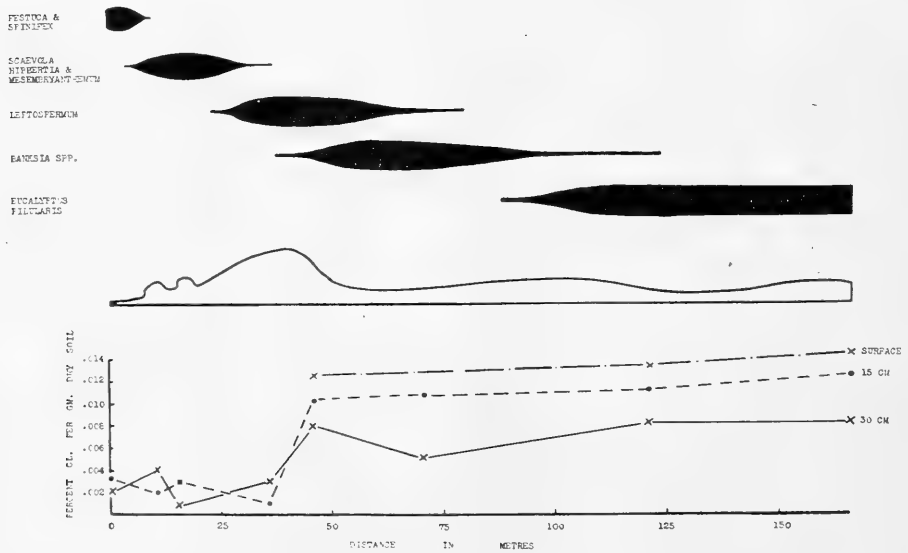
In the central coastlands, the first line of fixed dunes, the shrub dunes, are the highest and these are often succeeded by a series of old forest-covered dunes with an undulating appearance. On the small beaches, the dune series is usually limited to a shrub dune, behind which is a very restricted area of *Banksia* or *Eucalyptus* forest.

When the first line of shrub dunes reaches a definite height, it is almost always partially destroyed by a severe wind storm. Frequently fires are initially responsible for opening the way to wind destruction. With the formation of a "blow-out" or gap in the dune the loose sand is blown over the crest and subsequently buries part of the scrub thickets. Colonization recommences with the grasses and mat plants, and it is these habitats in which *Hibbertia* and *Scaevola* are particularly active (Pl. vi, fig. 2). Thus dunes are constantly in a state of flux; succession is partly progressive and partly retrogressive. On any large beach, one section of the shrub dunes is almost always undergoing secondary colonization.

(*b*) *Changes in the Environment.*

The most important environmental changes in sand-dune succession are the stabilization of the shifting sand and its enrichment by organic remains.

In the central coastlands, wind-blown sands are derived chiefly from Triassic and Permian Sandstones. They are white in colour and usually contain a high percentage of quartz and calcium carbonate. Under cover of vegetation organic matter is added and the sand becomes predominantly grey in colour. The composition of wind-blown sand from the strand stage is given in Text-figure 2. Apart from the increase in organic matter, there is no significant variation in the mechanical composition of the dune soils from the initial phase to the climax.

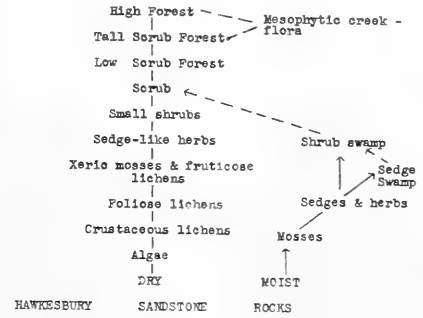


Text-fig. 9.—Graph showing relation between salt concentration (as % Cl. per gm. dry soil) at various soil depths, and distribution of dominants in seral stages of sand dune succession. (N.B.—Surface estimations not made in areas of loose wind-blown sand.) Central diagram represents physiographic outline of dune.

Text-figure 9 shows that the chloride content of dune soils increases with distance from the sea. This is explained by the fact that the humus content of the sand increases with distance from the sea; the leaching of chlorine ions is not only minimized by the presence of humus in the soil, but it was found by experiment that humus actually retains the chlorine ions. The experiment was as follows: Sand dune soils (*a*) with 2·4% humus, (*b*) sand without humus, were freed from all chlorides by shaking, washed with 2% NaCl solution, then washed in distilled water and air-dried. Subsequent chloride estimations showed that soil (*a*) contained ·06% chlorine per gram dry soil, but soil (*b*) contained no chlorine. The chloride content is highest in the *Leptospermum* thickets and hind-dune forest, where the humus content is highest (about 5%). As would be expected, the chloride content decreases with depth in these humified sands, whereas in sand with little humus (grasses and mat stages), leaching is more efficient, and in general the chloride content increases with depth. Text-figure 9 (stations 2 and 4), at an approximate distance of 12 and 37 metres, also indicates that leaching is most pronounced on hummocks and on the top of the dune.

This increase in salt content with distance from the sea is an interesting feature, but it must be remembered that the foredune and windward face of the fixed dune are subject to great fluctuations in chloride content; during heavy storms salt spray increases the salinity of the sand, which remains high until after leaching by rain.

(v) *Succession on Hawkesbury Sandstone Rocks.*



Text-fig. 10.—Diagrammatic representation of succession on Hawkesbury sandstone rocks.

(*a*) *Succession.*

A detailed description of the succession on Hawkesbury Sandstone has already been published (Pidgeon, 1938). It has not, however, been put into its setting in relation to other types of primary successions; nor has there been published any analysis of the peculiar difficulties which accompany the classification of vegetation in this sere.

In contrast to the types of succession already described, the succession on sandstone, except for the initial stages, is not set out in horizontal zonation. The sandstone vegetation consists of a mosaic of communities of which the most extensive are scrub-forests, characterized by well developed undershrubs. Scrub-forests are interrupted on the less favourable areas of the plateau surface by scrub and swamp communities, and in the more favourable areas such as gullies

by taller forests and patches of mesophytic vegetation. By a careful study of this mosaic of communities, it is possible to piece together the probable succession (Text-fig. 10).

The normal sere on sandstone begins on dry rocks; owing to local seepage or inadequate drainage some rocks are moist. Here the succession is either characterized by a less xeric flora, e.g. in the vicinity of creeks, or in extreme cases where water accumulates to give a high water table the sere is deflected and culminates in a swamp. Swamps, usually of very limited extent, occur frequently on the plateau surface. Unless conditions of drainage are modified, these swamps will probably persist unaltered and therefore may be regarded as deflected successions. The ultimate composition of any particular swamp varies with the degree of soil saturation. Where the ground is waterlogged for the greater part of the year, sedges occur belonging to the families Cyperaceae and Restionaceae (sedge swamp). The drier but still swampy areas are occupied by a number of moisture-tolerant shrubs in addition to the sedges (shrub swamp). (For floristics see Pidgeon, 1938, pp. 17, 18.)

On dry rocks the trend of succession is towards a tall Mixed *Eucalyptus* Forest (Pl. viii, figs. 3, 4), but the sere is arrested at various stages of development by locally unfavourable habitats, so that apparently permanent and mature communities such as scrub and scrub-forest persist over parts of the area.

On dry rocks there are the familiar types of pioneers: algae, crustaceous, foliose and fruticose lichens, mosses, tufted or sedge-like herbs and stunted leptophyllous shrubs. This succession of life forms is accompanied by a changing environment. The roots and rhizoids of the plants, assisted by weathering, disintegrate the rock and so form a sandy soil which is enriched by organic remains. The initial stages outlined above are frequently to be seen in lateral sequence on rock ledges (Pl. viii, fig. 2). Less commonly they occupy depressions in rock outcrops and form islands of vegetation. They may also form crevice communities, succession here being arrested until the surrounding rocks are colonized. On vertical rock faces there is a much richer lithophytic flora including orchids and ferns. (For floristic composition of these initial stages see Pidgeon, 1938, pp. 5, 6.) Most of the herbs have rhizomes and consequently spread rapidly once they are established in the moss mats. By the invasion of leptophyllous shrubs, the herb community passes into a low shrub phase, which in turn develops into a scrub community by the invasion of additional species. Contrary to its application in other areas, the term "scrub" as used here does not include tree species; it consists of a large variety of sclerophyllous, evergreen, woody shrubs, and although a number of herbs are present, much of the actual surface of the ground is bare. The scrub flora consists of approximately two hundred species (see Pidgeon, 1938, pp. 10, 24, 25), but it is noteworthy that most of the herbs belong to the families Cyperaceae, Restionaceae and Liliaceae and the shrubs to Proteaceae, Leguminosae, Myrtaceae and Epacridaceae.

If colonization has taken place in an unfavourable habitat, e.g. exposed to strong westerly winds, and where the soil remains shallow and with a low water-retaining capacity, the succession is arrested at the scrub stage. Consequently scrub covers a large area of the plateau ridges and coastal headlands. The height of the scrub varies from about 50 cm. to 3 metres according to the degree of exposure; a low rosette-growth is typical of coastal headlands.

On the other hand, if colonization has taken place in an area where conditions would eventually be favourable to the development of trees, the scrub community

is only a seral stage to the development of forest. Evidence for this is in the occurrence of patches of scrub vegetation in which young trees are developing. The height and species of the trees present are apparently controlled by soil moisture conditions, which are in turn determined by aspect and colloidal soil content. It is convenient to consider three physiognomic forest types, although many gradations occur. These are low and tall scrub-forest and high-forest.

Low scrub-forests range up to 9 metres in height; they are open in structure and are characterized by a well-developed shrub layer, consisting of much the same species as comprise the scrub flora. The chief dominants are *Eucalyptus haemastoma*, *E. micrantha* and *E. gummifera*; other species are listed in Table vi. These forests cover a large area of the uplands and rocky slopes. Tall scrub-forests differ from the preceding type in that the tree canopy is more continuous and reaches an average height of 16–20 metres. The chief dominants are *E. gummifera*, *E. piperita*, *E. Sieberiana* and *Angophora lanceolata* (see also Table vi). These forests occur on sheltered areas of the uplands and on gully slopes. The shrub strata consist of sclerophyllous types, many of which are the same species or different species of the same genera which occur in scrub. In addition the herb flora is more abundant than on the plateau surface and there are several creepers.

TABLE vi.

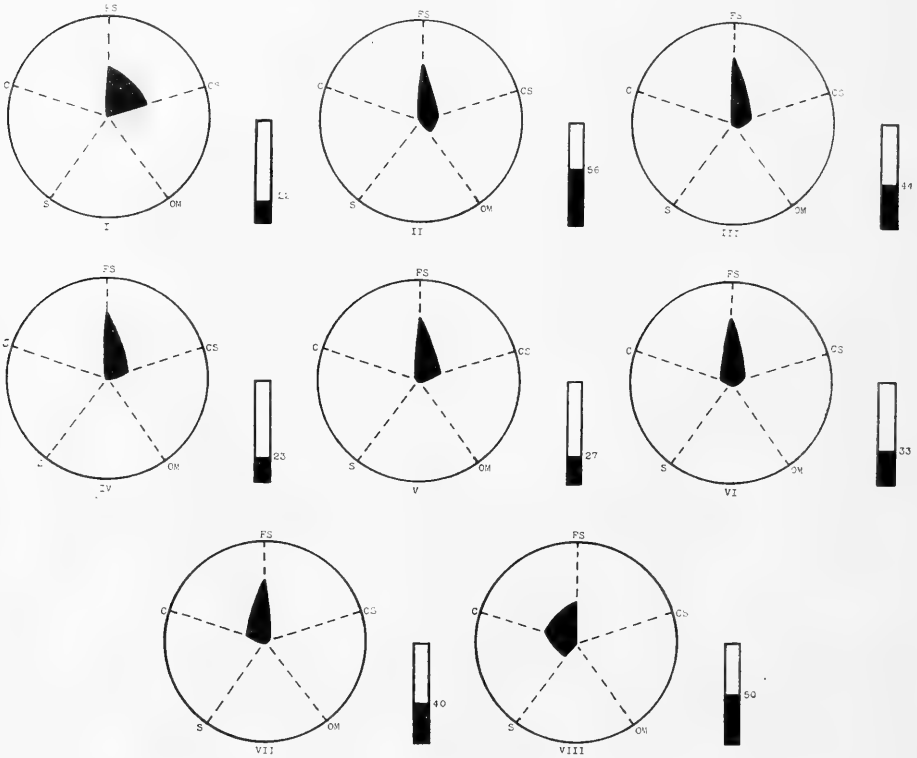
Occurrence of the Most Important Trees in the Various Structural Forest Types on Sandstone.

Species.	Low Scrub-Forest.	Tall Scrub-Forest.	High-Forest.
Dominants.			
Eucalyptus haemastoma Sm.	x		
E. eximia Schauer	x		
Angophora Bakeri C. Hall	x		
E. capitellata Sm.	x	o	
E. eugenioides Sieb.	x	o	
E. micrantha DC.	x	o	
E. gummifera (Gaertn.) Hochr.	x	x	
E. punctata DC.	o	x	
E. Sieberiana F.v.M.	o	x	
E. umbra R. T. Baker	o	x	
Angophora intermedia DC.		x	
E. piperita Sm.		x	o
A. lanceolata Cav.		x	x
E. pilularis Sm.			x
Syncarpia laurifolia Ten.			x
Sub-dominants.			
Casuarina suberosa Ott. & Dietr.	o	x	
C. torulosa Ait.		o	x
Banksia serrata L.	x	x	

x indicates typical occurrence; o indicates occasional occurrence.

In high-forest (Pl. viii, fig. 4) the trees average 26–32 metres, and in the sandstone country such a forest is in most cases limited to gullies owing to its high soil-moisture requirement. The dominant tree is *E. pilularis*, which is often associated with *Angophora lanceolata* and *Syncarpia laurifolia*. In high-forest the undershrubs consist mainly of species which are restricted to gully habitats;

they may still be termed sclerophyllous, but their leaves are not nearly so hard as in those species which occur in scrub communities. Herbs and creepers are also abundant and ferns form local societies. High-forest is not found in every gully; moreover in narrow gorges its distribution is limited near creeks by the development of mesophytic communities which are favoured by the increased shade and high humidity. These mesophytic types are allied to sub-tropical rain-forest species (see Pidgeon, 1938, p. 15).



Text-fig. 11.—Diagrammatic representation of mechanical analysis of sandstone soils at various stages of succession. Typical mature shale soil from *E. saligna-E. pilularis* forest included for comparison. The percentage coarse sand (CS), fine sand (FS), silt (S), clay (C) and organic matter (OM) are plotted along the 5 axes of the circle, the radii of which represent 100%.

In most cases, the data are averages of the analyses from the various horizons. The following stages of succession are represented: I, Sandstone rock (bare); II, Moss Mats (soil 10 cm. deep); III, Shrubs and herbs (soil 10 cm. deep); IV, Scrub (average from analyses of samples taken at depths of 0-10 cm. and 15-20 cm.); V, *E. haemastoma* scrub-forest (average from analyses at 0-5 cm., 15-20 cm. and 40-45 cm.); VI, *E. piperita* forest (average from analyses at 0-5 cm., 15-20 cm., and 40-45 cm.); VII, *E. pilularis* forest (average from analyses at 0-10 cm., 20-33 cm., 45-58 cm., 58-68 cm.); VIII, *E. saligna-E. pilularis* forest (average from analyses at 0-18 cm., 45-55 cm., 80-93 cm.).

Stages I to IV are a horizontal series from rock ledge to scrub, and V to VII are from the gully represented in Text-fig. 13.

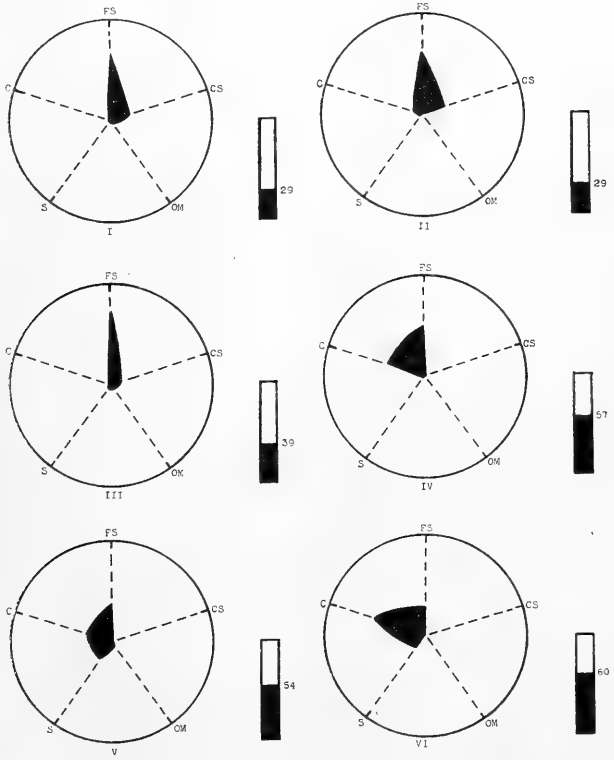
Maximum water-retaining capacity (field capacity) of the soils is indicated by the shaded area in the rectangular block which represents 100 per cent. The values given are averages where the mechanical analyses represent averages.

An illustration of the value of trees as plant indicators is given by Table vi, which shows how forests developing in the same climate under different physiographic conditions have different floristic composition (see also Text-fig. 13).

(*b*) *Changes in the Environment.*

The Hawkesbury Series consists of siliceous sandstones with aluminous or ferriferous clay as the cementing material. They yield light-coloured sandy soils of low water-retaining capacity; the initial rock, represented in diagram i of Text-figure 11, has only 6% clay and silt fraction.

The soil changes typical of sandstone succession are represented diagrammatically in Text-figures 11 and 12. There are no outstanding changes in pH values. The first formed soil contains a fairly high percentage of organic matter from lichen and moss plant residues. As the sandstone disintegrates, the percentage of sand increases again, until in the scrub stage the mechanical composition of the soil is little altered from the initial rock, except for the



Text-fig. 12.—Diagrammatic representation of mechanical analysis of various horizons from profiles of *E. haemastoma* and *E. pilularis* forest soils (sandstone) and *E. saligna-E. pilularis* forest soil (shale). Averages of these profiles are given in Text-fig. 11. The horizons represented are as follows: I, A horizon (0-5 cm.) in *E. haemastoma* forest; II, B horizon (35-60 cm.) in *E. haemastoma* forest; III, A horizon (0-10 cm.) in *E. pilularis* forest; IV, B-C horizon (58-68 cm.) in *E. pilularis* forest; V, A horizon (0-18 cm.) in *E. saligna-E. pilularis* forest; VI, B-C horizon (80-93 cm.) in *E. saligna-E. pilularis* forest.

Water-retaining capacities of the soils at the various horizons are also shown.

addition of a small amount of organic matter.* Diagrams v to vii in Text-figure 11 emphasize the limiting effect of the soil factor in the development of the various types of forest. The organic matter and clay fractions increase markedly from the *E. haemastoma* stage to the *E. pilularis* stage. Concurrent with the changes in the mechanical composition, the water-retaining capacity rises sharply with the increased organic matter in the moss stage, and falls again in the scrub stage. With increased amounts of organic matter and clay fractions in the forest soils, it gradually rises to a second maximum in the *E. pilularis* forest.

Text-figure 12 emphasizes certain aspects of the development of forest soils which are partly obscured in the generalized diagram of Text-figure 11. The most important point is the marked accumulation of clay (40%) in the B horizon of the *E. pilularis* soil as compared with the significantly smaller amount (10%) in the *E. haemastoma* soil. Although the accumulation of clay in the lower horizons of any profile is a leaching effect, it must be remembered that the initial composition of the rock varies considerably; the intercalation of shaly bands in the sandstone strata is a marked feature.

Discussion and Conclusions.

(i) *Classification of the Vegetation on Sandstone.*

By use of the technique of plant succession it has been possible to make a comprehensive classification of vegetation on sandstone. The method however is less successful here than in America and Europe. The reasons for this will become apparent in the following pages.

Throughout this discussion it is essential that the broader aspects of classification are not obscured: the climax formation of the south-eastern coast of Australia is *Eucalyptus* Forest. This formation is unique in that there is only one dominant genus—*Eucalyptus*. Several associations of this formation are represented on the central coastlands, but the Mixed *Eucalyptus* Forest Association typical of sandstone soils covers by far the largest area. This Association differs from the typical coastal forests in the stunting of the trees (average height, approx. 15 metres), the open canopy, the well developed shrub strata, and relative absence of herbs and grasses. Usually several dominant species occur in any one stand. A low degree of integration in these forests is indicated by the fact that they frequently merge almost imperceptibly into scrub communities. The *Eucalyptus saligna–E. pilularis* Association is typical of the coastal forests, and its structure provides a useful basis of comparison with the sandstone forests. In the central coastlands, its occurrence is limited by the soil factor, but it is one of the most widespread of the coastal associations. In this district it occurs on loams and clays derived from Triassic Wianamatta Shales which form isolated cappings on several ridges on the sandstone plateau, and from Narrabeen Shales which form most of the coastal plains. The trees are tall (25–50 metres), the canopy is usually continuous, but a considerable amount of sunlight penetrates to the ground owing to the peculiar orientation of *Eucalyptus* leaves. The undergrowth forms a fairly continuous ground cover of herbs and grasses with a scattered assemblage of shrubs, most of which are sclerophyllous. The shrubs vary in height from about 1 to 5 metres.

The first difficulty in the classification of sandstone forests is that the individual tree species rarely occur in pure stands; mixed stands of several species

* Initial rock stage i: total sand, 93·7%; organic matter, 0; scrub stage, iv: total sand, 86·0%; organic matter, 7%.

are characteristic; consequently one cannot speak of consociations or consocies with regard to sandstone forests, although this is possible elsewhere on the coast of New South Wales (Pidgeon, 1937). However, the concept of forest types is very useful, forest type being defined as a stand of trees of distinctive floristic composition. On sandstone, typical forest types consist of two or three species, of which the following groupings are typical: *E. haemastoma–E. micrantha*, *E. haemastoma–E. gummifera*, *E. gummifera–E. piperita*, *E. piperita–A. lanceolata*, *A. lanceolata–E. pilularis*, *A. intermedia–E. punctata*. These are equivalent in rank to Clements' (1936) faciations and lociations; considered as a whole, they comprise the Mixed *Eucalyptus* Forest Association. This matter will be discussed more fully in Part iv of this series of papers.

The factors which complicate the successional analysis of the sandstone vegetation may be summarized as follows:

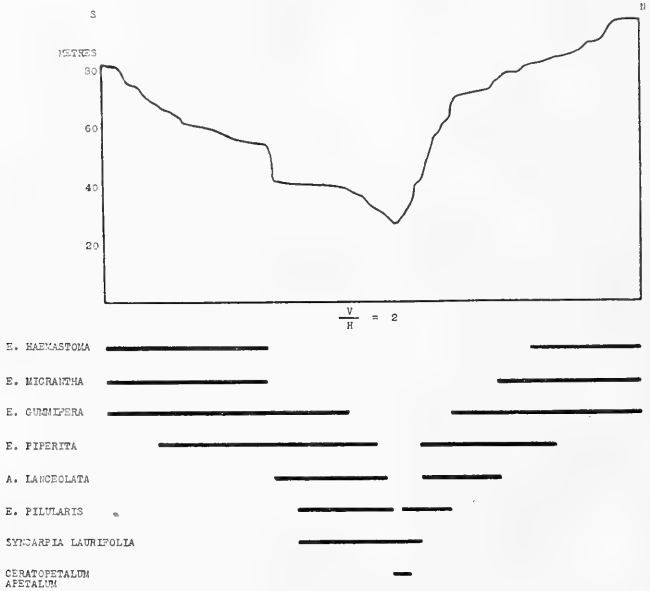
(*a*) Unfavourable soil conditions.
(*b*) Immaturity of landscape and soils coupled with dependence of succession on physiographic changes.
(*c*) Prevalence of fires.
(*d*) Instability of vegetation even at climax.
(*e*) Large number of tree species.

(*a*). The Mixed *Eucalyptus* Forest Association is definitely limited by unfavourable soil conditions of low mineral content and poor water-retaining capacity. Although the sandstone country receives a mean rainfall of approx. 1100 mm., drainage through the porous soils is very rapid; consequently there are periods of soil drought as well as atmospheric drought, the latter being induced by extreme insolation and exposure to desiccating winds. Consequently it is not remarkable that these forests comprise a distinct association type characterized by an average low stature and by a vigorous growth of shrubs. The shrubs have tough leathery leaves with xeromorphic characters and a hard internal skeleton of fibres which enables them to survive without showing signs of wilting during conditions of water shortage.

(*b*). The initial stages of dry rock succession leading to the development of scrub are a true autogenic succession. Deficiencies in water and nutrients become less extreme by the formation of soil, whilst the shade afforded by the developing vegetation reduces the temperature extremes, and increases the relative humidity. After these pioneer stages, which may appear as zoned communities, there are no clear seral stages; succession runs parallel with physiographic change and soil development (see Text-figs. 11 and 12). From ridge top to gully bottom there is a spatial sequence not only of structural communities, but of *Eucalyptus* species. This is illustrated by Text-figure 13.

The Hawkesbury Sandstone area is characterized by juvenile physiography and immature soils. The cycle of erosion is very slow; geological evidence indicates that it is slower than in the past because the rainfall is lower and consequently the streams have diminished considerably in volume. The youthful physiography of the sandstone plateau and the comparative hardness of the Hawkesbury rock strata have resulted in shallow soils characterized by truncated profiles. In most cases the soils are too immature to be termed podsols, but zonal development is usually sufficient to show an accumulation of humus of varying depth and an iron accumulation in the B horizon. A sandy soil with a high percentage of humus gives extremes of profile development, and in many cases the accumulation of colloidal material is insufficient to arrest the leaching

process; consequently the various horizons are often diffuse and difficult to determine. There is not a continuous soil cover; the dissection of the plateau has resulted in the exposure of a large amount of rock. Over much of the area soil development and accumulation is negligible or proceeds comparatively slowly; in fact, new rock is being continually exposed; on the plateau strong winds remove a considerable amount of soil and sweep away weathered particles from



Text-fig. 13.—Distribution of trees in relation to exposure in a sandstone gully. The upper line represents the section of the gully; the lower lines represent the distribution of the trees. Data plotted from transect 15 metres wide. N = North, S = South. The author is indebted to Miss I. Burke and Miss N. O'Grady for collecting these data.

rock exposures; on steep slopes run-off water is an important agent of soil removal. Thus, owing to unfavourable physiographic conditions, it is only on the gentle slopes of gullies that soil development proceeds to any depth. Accordingly, apart from the initial stages, there may be little or no plant succession, but rather a series of dynamic equilibria between vegetation and habitats. From these many stages it is possible to piece together the probable succession which in favourable situations has led to a climax, but it does not seem legitimate to assume that each of the seral stages* is itself moving toward a climax. Much of this immature forest vegetation is to be interpreted rather as a number of sub-climaxes arrested at one stage or another by habitats conditioned by the physiography. Because of the immature physiography, succession is often retrogressive: in forests on steep slopes, erosion results in continuous exposure of new rock surfaces, so that here, succession is partly retrogressive, whilst lower down the slope where the soil is deposited, succession is accelerated. On some rock outcrops, especially on ridges exposed to wind and rain, succession is not progressive, because soil has no chance of accumulating.

* It is impossible to apply quantitative methods in the analysis of forest stands because annual rings are not a constant feature and girth measurements are too variable.

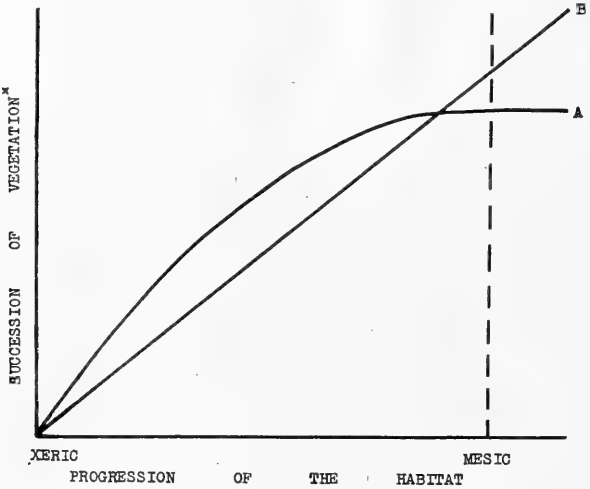
(*c*). This arresting of succession by physiographic conditions is also accentuated by the continual destruction of the vegetation by regularly recurring fires. It is probably not incorrect to assume that all sandstone forests have at some time been partially destroyed by fire, and although recovery is remarkably rapid, the repeated burning in any one area over a number of years is reflected both in the structure and the composition of the vegetation. Owing to the ability of *Eucalyptus* species to develop epicormic shoots which regenerate, few trees are actually destroyed by fire although they may become gnarled or stunted. The composition of the subdominant strata is frequently altered, either temporarily or permanently according to a complex of factors such as severity of fire, number of species capable of regeneration from vegetative parts, time of fruiting, etc. So although it may be said that a particular forest type is rarely reverted to an earlier stage through fire, it is probable that fire frequently retards progression.

(*d*) and (*e*). The most serious difficulty of all lies in the definition of the climax on sandstone, whereas in many districts in Europe and U.S.A. there seems little doubt about the determination of the climax itself. On sandstone it is possible to interpret the climax in at least three different ways: (i) All the mature forest types comprising the Mixed *Eucalyptus* Forest may be regarded as variants of one climax; (ii) alternatively the various types of mature forest may be regarded as subclimaxes arrested more or less permanently short of a climax which is represented by high forest of *E. pilularis*, or (iii) a climax is not attained anywhere on the sandstone.

(i). If all the mature forests are interpreted as variants of one climax then this climax is not equivalent to the beech forest climax in England or the beech-maple forests in parts of U.S.A., because on Hawkesbury sandstone every small area of micro-climate has its own local variation of climax. The species of *Eucalyptus* are remarkably sensitive indicators of climatic conditions, particularly of water balance, and vary from place to place with changes in aspect and water-retaining capacity of the soil. For example, a protected slope carries a different tree flora from a level stretch of sandstone on top of the plateau, and even on a plateau the forest type may vary. The reflection of the micro-climate in the tree flora is possible only because of the large number of species of *Eucalyptus*. Such a floristic variety is not encountered in European climaxes. This interpretation of climax blurs the concept of succession tending toward a definite climax type. For example, the climax forest on clay in Southern England is *Quercus*, both in Hertfordshire with a rainfall of approximately 650 mm. and in Gloucestershire with a rainfall of approx. 1000 mm. By contrast, in the Sydney district, mature soil derived from shale 10 miles from the coast, with a rainfall of 1200 mm., carries *E. saligna–E. pilularis* forest and the same shale ten or twenty miles further inland with a rainfall of less than 800 mm. carries *E. tereticornis–E. hemiphloia* forest. The sensitivity of the sandstone forests to local changes in climate compared with the stability of the climaxes in other regions may be represented schematically by Text-figure 14. Clearly, one cannot speak of this "climax" on Hawkesbury Sandstone in the widely accepted sense of the word "climax". *So long as the composition and physiognomy of the tree stratum fluctuates with every variation in local climate, it seems undesirable to regard the vegetation as climax* (Text-fig. 14).

(ii). If one accepts the climax as high forest of *E. pilularis*, comparisons show that this forest type approaches more to the structure of the coastal *Eucalyptus* climax forests than any other sandstone forest. Also, there is sufficient

evidence to show that of all the tree species found on sandstone, *E. pilularis* has the highest soil moisture requirements, and it is the only sandstone species which is a dominant of the *E. saligna–E. pilularis* Association. In addition, *E. pilularis* ranges throughout the formation as a dominant occurring in many associations.



Text-fig. 14.—Schematic diagram showing the relation of succession to climate in Great Britain or Chicago (A) and on Hawkesbury Sandstone, N.S.W. (B). * No quantitative measure possible, but height is a first approximation.

The interpretation of *E. pilularis* high forest as the climax is supported by the following: In the Sydney district, there seems little doubt that the factor limiting vegetation is water balance, and this is particularly true of vegetation on sandstone. Now the more favourable the water balance, the more likely it should be that the curve of "succession–climate" (Text-fig. 14) becomes concave to the climate axis, i.e. the less sensitive will the mature vegetation be to local variations in climate. This proves to be the case, for on loams derived from Wianamatta Shales with the same rainfall as that occurring on sandstone, the water balance is much more favourable and there is practically no response of the *E. saligna–E. pilularis* Association to local climatic variations: a high forest of *E. saligna*, with or without *E. pilularis*, occurs both on the ridges exposed to strong westerly winds and on the sheltered slopes. On sandstone, the same variations in aspect are reflected in the vegetation—scrub or low forest of *E. haemastoma* on the ridge, and a taller forest of *A. lanceolata*, *E. piperita* or *E. pilularis* on the sheltered slope.

(iii). If the view is taken that the climax on sandstone will be developed only in areas of mature physiography and mature soils, i.e. when the plateau is worn down to base level, then unless it postulates the development of a more advanced type of forest than *E. pilularis*, this interpretation may be dismissed on the following considerations: The evidence suggests that sandstone vegetation on mature physiography would not include species higher in the scale of succession than *E. pilularis* because:

(*a*) Species such as *E. saligna* are restricted to richer loam soils; this is probably correlated with chemical as well as physical composition of the soil.

(*b*) *E. pilularis* is widespread on "podsolized" sandy loams on the undulating coastal plains, i.e. in areas of comparatively mature physiography.

(*c*) The presence of *E. pilularis* on shale ridges exposed to westerly winds indicates that this species can stand exposure and that its general restriction to gullies in sandstone country is determined by soil moisture requirements. This is also supported by the occurrence of a fairly extensive patch of *E. pilularis* high forest south of Sydney on the sandstone plateau bordering the scarp, about 90 metres above sea level. Although this habitat is more exposed than usual for *E. pilularis* on sandstone, it is compensated by a high rainfall (over 1300 mm. per annum) and by frequent mists.

(*d*) The water-retaining capacity of a mature sandstone soil, enriched by humus and showing signs of podsolization, compares fairly favourably with that of a shale soil (see Text-figs. 11, 12). At present, owing to physiographic conditions, soils in this state of development are limited to lower slopes and gullies, or if they occur on flat areas on the surface of the plateau they are badly drained and are therefore characterized by semi-swamp forests. With the development of a mature physiography on sandstone, it is reasonable to expect a parallel soil development and therefore a more widespread occurrence of high forest.

It may be concluded that the major difficulties encountered in the successional analysis of the Hawkesbury Sandstone vegetation are:

(i) The fact that plant succession runs parallel with physiographic shelter and soil development, and since these factors seem to be comparatively stable, the vegetation forms a mosaic of subclimaxes.

(ii) The fact that the climax is difficult to interpret because of the unfavourable soils, immature physiography and large number of tree species, which results in a sensitivity to micro-climate not found in the climax associations in some other regions.

According to the interpretation of climax as the stable types or the most advanced type of *Eucalyptus* forest, the climax is (*a*) a mosaic of forests of which every small area of micro-climate has its own local variation of climax, or (*b*) high forest of *E. pilularis*.

(ii) *General Conclusions.*

In the central coastlands it is evident that primary xerarch and hydrarch successions* result in the development of Mixed *Eucalyptus* Forest, and that in the successions on sandstone rock and wind-blown sand the climax forest type is often *E. pilularis*. The hydrarch successions have been traced only to relatively small stands of mixed forest, and in the particular seres investigated *E. pilularis* has not often been recorded.

North and south of the central coastlands, which correspond approximately to the area flanked by the Hawkesbury Sandstone plateau, no departure is found from the recorded successions on dunes and in salt and brackish swamps, with the exception that the climax *Eucalyptus* forests of the swamp seres are not Mixed *Eucalyptus* Forest types. This variation is only to be expected because the actual species which invade the swamp mahogany forest depend partly on the initial physical and chemical composition of the mud bank (which in the final stage becomes the area occupied by forest), and on the nature of the soil from the

* With the exception of freshwater river succession and some brackish swamp seres noted above.

surrounding hills and slopes which is washed on to the swamp by means of drainage water. On the central coastlands, where the mud banks are composed of coarse sand and silt, and the surrounding country is chiefly sandstone, it is reasonable to expect forest types of the Mixed *Eucalyptus* Forest Association to succeed *E. robusta*. On the other hand, in the Port Stephens estuary (north of the central coastlands), the mud banks are formed of heavy clay and silt, and here the climax forest of the salt swamp sere is frequently entirely different;* so also are the rocks, soil types and *Eucalyptus* Associations of the surrounding hinterland. The climax forests on sand dunes are fairly constant, since the initial composition of the sands is essentially similar; the variations which do occur are determined by latitudinal range of species and local habitat variations.

Thus, throughout most of the New South Wales coast, although the trend of primary successions in water and on wind-blown sands is always towards *Eucalyptus* Forest, the specific composition of the climax forest of any particular sere varies according to the local expression of the climatic climax *Eucalyptus* Forest and, as previously stated, soil type is chiefly responsible for these variations.

In the writer's opinion, the most satisfactory interpretation of the sandstone vegetation of the central coastlands is as follows:

(i) The Mixed *Eucalyptus* Forest Association may be regarded as an edaphic climax association, i.e. the sandstone forests (with the exception of *E. pilularis* type) are not a typical expression of the coastal *Eucalyptus* forests which comprise the climatic climax formation.

(ii) Most of the sandstone forests are sub-climaxes, conditioned by the physiography through soil development and subsequently soil moisture.

(iii) *E. pilularis* high forest is the climatic climax forest type on sandstone; it is of limited occurrence and is developed only under optimum soil-moisture conditions.

Summary.

Five types of primary succession occurring in the central coastlands of New South Wales are summarized. These are the seres which begin on salt mud flats, in brackish water of lagoons, in fresh water, on wind-blown sand, and on sandstone rock.

The convergence of these seres to the same climax, viz. Mixed *Eucalyptus* Forest, is discussed.

The environmental factors influencing the successions are briefly referred to. In particular, various aspects have been studied of the soil changes which accompany succession.

Difficulties in the application of the concept of succession to the classification of the vegetation of the central coastlands are discussed.

Acknowledgement.

It is with pleasure that the author acknowledges her indebtedness to Professor Eric Ashby of the Botany Department, University of Sydney, for his invaluable suggestions and criticisms during the progress of the work and in the presentation of this paper.

* E.g., a typical climax includes *E. amplifolia* and *E. tereticornis* or *E. paniculata* and *E. maculata*, etc.

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DESCRIPTION OF PLATES VI-VIII.

Plate vi.

Fig. 1.—Miniature dunes formed by *Senecio spathulatus.*

Fig. 2.—Dune partially destroyed by series of "blow-outs" undergoing secondary colonization. Foreground: mats of *Hibbertia volubilis* and *Scaevola suaveolens*; middle ground: tufts of *Lomandra longifolia* and *Scirpus nodosus*, also remnants of dense dune scrub. Series of hummocks of *Festuca littoralis* bordering ocean front.

Fig. 3.—Foredune of tufted *Festuca littoralis* and runners of *Spinifex hirsutus.*

Fig. 4.—Brackish-water succession at lagoon edge. *Phragmites communis* and line of *Casuarina glauca.* Isolated tufts of *Juncus maritimus* in foreground.

Plate vii.

Fig. 1.—*Salicornia australis* meadow and fringing forest of mangroves: *Avicennia officinalis* present as trees and also in dwarf form mingling with low shrubs of *Aegiceras majus.*

Fig. 2.—Stages of salt marsh succession; *Salicornia australis* succeeded by zones of *Juncus maritimus, Melaleuca ericifolia,* and forest stages, including *Casuarina glauca, Melaleuca Leucadendron* and *E. Kirtoniana.*

Fig. 3.—Freshwater swamp in wind-blown sand at Port Stephens. Reed stages, chiefly *Lepironia mucronata,* being invaded by *Melaleuca Leucadendron* (left foreground). Swamp surrounded by *Melaleuca* and sand-dune forest.

Fig. 4.—*Banksia serrata* dune forest with ground stratum of *Pteris aquilinum.*

Plate viii.

Fig. 1.—*Melaleuca Leucadendron* swamp forest with sub-dominant stratum of *Cladium junceum* and *Gahnia* spp.

Fig. 2.—Stages of Hawkesbury sandstone rock succession in lateral zonation. Foreground: moss mats with tufted herbs and low shrubs; middleground: tall shrubs and trees with *Eucalyptus haemastoma* at right.

Fig. 3.—Mixed *Eucalyptus* Forest on sandstone. *E. gummifera* (dark trunks) and *Angophora lanceolata* (white trunks).

Fig. 4.—High forest of *E. pilularis* on sandstone. Odd trees of *Angophora lanceolata* in middle ground.

FURTHER OBSERVATIONS ON THE TROMBIDIID LARVAE OF NEW GUINEA (ACARINA, TROMBIDIIDAE).

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(Fourteen Text-figures.)

[Read 31st July, 1940.]

Since the material for previous papers on this subject was prepared, further observations and records have been made. In this paper it is proposed to follow the arrangement of the writer's "Trombidiid Larvae in New Guinea" (1939), thus making the present one supplementary to it.

Names of Species.

It has been necessary to make two alterations in the names of species previously described. By a mischance the name *Neoschöngastia kallipygos* was rendered invalid, and in a recent paper (1939*a*) the name *Neoschöngastia bipygalis* was substituted. Womersley then (1939) erected the genus *Guntheria* to accommodate this species. In another paper (1939*b*) *Trombicula hirsti* variety *buloloensis* was identified with *Trombicula minor* Berlese 1905, the former name becoming a synonym. In addition, Womersley has erected another new genus, *Paraschöngastia*, to accommodate four species described by the writer as belonging to the genus *Neoschöngastia*—*Paraschöngastia yeomansi*, *P. retrocincta*, *P. backhousei*, and *P. dubia*.

General Considerations.

Thanks to the kindness of Dr. F. J. Williams, Chief Medical Officer of Papua, and various members of his staff, I have been able to ascertain that larval mites abound in Papua, but that none have been noted in the dry belt around Port Moresby, while they are uncommon around Misima. Mr. G. W. Lupson of Port Moresby, in a personal communication, states that in the Delta Division "scrub itch" is common, and that it is caused by a larval mite resembling *Trombicula hirsti*. Papuan natives appear to suffer more severely from the attacks of mites than do those of the mandated territory. Their names for them are *tigali*, *sanana* (Motuan), and *dedigalogala* (Luan).

Mr. H. Horne, of the Bulolo Gold Dredging Field Staff, informs me that mites are abundant in the southern part of Dutch New Guinea; and that none are to be found on the Ramu plateau in the mandated territory, which is at an altitude of over 5,500 feet. Recently, in collaboration with Schroeder of Wewak, the writer reported (1939) that the whole of the Sepik District is heavily infested with mites, and that many of the islands off the coast of this district abound with such remarkable numbers that they are called locally "*mokka*-islands".

The finding of colonies of larvae inside the ears of rats, wallabies, bush fowl, and bush turkeys, brings the New Guinea mites in line with those of other countries.

Technique.

Although gum-chloral is infinitely superior to canada balsam for studying detail, it tends to cause specimens to swell so much that after a short time the relationships of certain features are altered, and some of the measurements are increased to an extent which might lead to inaccuracy; it is wise, therefore, to make parallel mounts in balsam, from which to check the gum-chloral preparations.

Hosts.

The following additional records of the occurrence of larvae on known hosts from Bulolo are presented:

1. Bush fowl (*Megapodius duperreyi*): *Trombicula rioi*, *Paraschöngastia retrocincta*, and *P. yeomansi*, all in colonies on the legs; and *Schöngastia blestowei*, in colonies inside the ears.
2. Brown's rat (*Rattus browni*): *Neoschöngastia impar*, in rows along the margins of the ears; *Walchia morobensis*, embedded in the nose; and a new species, *Trombicula vanderghinstei*, in colonies inside the ears.
3. Man: Additional specimens of *Trombicula minor*, making a total of 64 from 9 men; and additional specimens of *Schöngastia blestowei*, making a total of 54 from 8 men. In two instances both species were present on the same host at the same time.

The following new hosts have been recorded from Bulolo:

1. Scrub wallaby (a local highland form of *Macropus* (*Thylogale*) *coxeni* Gray 1866): A colony of 5 specimens of a new species, *Schöngastia taylori*, on the scrotum of one, and many colonies of this species on the legs of another; two new species, *Neoschöngastia womersleyi* and *N. foliata*, in colonies inside the ears of two.
2. Brown scrub rat (a local variant of *Rattus mordax* (*sensu lato*) Thomas 1904): *Guntheria bipygalis* embedded in the skin of the abdomen, and ova cemented to the abdominal hairs; colonies of *Trombicula vanderghinstei* inside the ears, on three examined.

Two species of snipe and one water-rat (*Hydromys oriens* Troughton 1937) were examined without finding any larvae.

In a recent discussion on the epidemiology of endemic typhus in New Guinea (1939*c*) it was found necessary to classify the hosts of certain larval mites according to the manner in which the various species are found to infest them; there are three categories:

a. The larvae occur in colonies composed of up to fifty, embedded closely together in hollowed-out pits in the skin. These pits are found regularly on certain hosts, and at constant sites.

b. Although no colonies in pits are found, the larvae occur regularly on certain hosts, in relatively large numbers, and at constant sites.

c. Occasional single specimens are found embedded here and there, not in colonies or groups, nor at constant sites, nor regularly on the same host.

I have designated the hosts in categories *a* and *b* as the "principal hosts", and those in category *c* as "casual hosts", and I propose to use these terms in these senses in the future.

Genus Paraschöngastia Womersley 1939.

Trans. Roy. Soc. S. Aust., lxiii, (2), 165.

PARASCHÖNGASTIA YEOMANSI (Gunther 1939). Fig. 1.

Neoschöngastia yeomansi, Gunther, PROC. LINN. SOC. N.S.W., lxiv, 1939, 81.

Coxae iii bear usually two setae, one on the anterior margin towards the medial end, and the other at the extreme antero-lateral angle, instead of only one as originally reported. This will necessitate altering the keys previously published (Gunther, 1939; Womersley, 1939).

Principal host: Bush fowl (*Megapodius duperreyi*), colonies on the legs.

PARASCHÖNGASTIA RETROCINCTA (Gunther 1939). Fig. 2.

Neoschöngastia retrocincta, Gunther, PROC. LINN. SOC. N.S.W., lxiv, 1939, 87.

The tubercles which form the circle surrounding the posterior pole of the body (described previously as "devoid of setae") carry setae in the younger larvae. These setae are from 50 to 57·5μ long, straight, stout, and covered with very short spines; they stand out from the body, pointing slightly backward. They are apparently not very secure, and in older specimens most or all of them may be missing. The chelicerae are slender, with a flattened S-curve; the dorsoapical tooth is a long fine barb pointing backward; the ventral tooth is sharp and prominent, level with the dorsoapical, pointing forward, and forming a continuation of a long ventral ridge. This confirms the provisional placing of this species in the genus *Neoschöngastia* originally. The setae on the cheliceral sheaths (previously described as "apparently nude") are long, slender, straight, and nude.

Principal host: Bush fowl (*Megapodius duperreyi*), colonies on the legs.

Key to the New Guinea species of Paraschöngastia.

1. Coxae iii with 3 setae. No pitted area posteriorly on dorsum. Scutal crest indefinite medially. Dorsal setae 96, arranged: 2, 14, 10, 12, 6, 14, 14, 12, 8, 4 .... *P. dubia* (Gunther 1939)
   Coxae iii with 1 or 2 setae 2
2. Coxae iii with 1 seta. Striations weak over posterior sixth of dorsum, with weak pitting over this area. Dorsal setae 72, arranged: 2, 14, 14, 10, 8, 8, 6, 6, 2, 2 ..... *P. backhousei* (Gunther 1939)
   Coxae iii with 2 setae. Posterior portion of body not striated, but pitted. The setae in this area arising from tubercles 3
3. Pitting over posterior fourth of body. Dorsal setae 100, arranged: 2, 16, 8(10), 12(10), 10(8), 10, 8(10), 12, 6, 6, 6, 4 (the last five rows arising from tubercles) ..... *P. yeomansi* (Gunther 1939)
   Posterior pitted area relatively small, and bounded anteriorly by a circle of tubercles bearing long straight setae (these setae may be missing in older specimens). Dorsal setae 64, arranged: 2, 8(10), 12(10), 6, 8(10), 8, 8(6), circle of tubercles, 12 (arising from irregularly placed oval tubercles) .. *P. retrocincta* Gunther 1939

Genus TROMBICULA Berlese 1905.

Redia, ii, fasc. 2, 155.

TROMBICULA VANDERGHINSTEI, n. sp. Figs. 3, 4, 5.

Body a long oval, widest at level of coxae iii; length, 354μ; width, 223μ; newly-hatched, 206μ × 112μ; largest seen, 370μ × 250μ. Colour pale orange. Striations fine and weak; pitting on scutum, maxilla, and coxae. Maxillary setae stout, with about 7 long fine branches. Chelicerae stout, tapering to a fine sharp point. Dorsoapical tooth single, subterminal, a mere rounded swelling. Ventral tooth opposite the dorsoapical, sharp, pointing backward. A stout seta on each cheliceral sheath, with a few long fine branches. Palpi rounded, but with a slight angulation at the curve of segment ii, and tapering fairly sharply. One long nude seta on ii; a nude seta near the base, and one, branched, near the

apex, on iii; on iv, one nude seta at the base, one (sometimes two) nude seta half-way, and one branched seta towards the apex. Appendiculum short, stout, bluntly rounded, with 6 or 7 setae: one short, stout, and nude, at the base; one very long, with long branches, towards the apex; and 4 or 5, fine, with fine branches, between. Palpal claw trifurcate, the central element very long, curved, with a sharp hooked point; the medial element shorter, very fine and sharp; the lateral element very short, blunt, and so closely applied to the central element as to be visible only in a few specimens. Scutum curved backward, with parallel

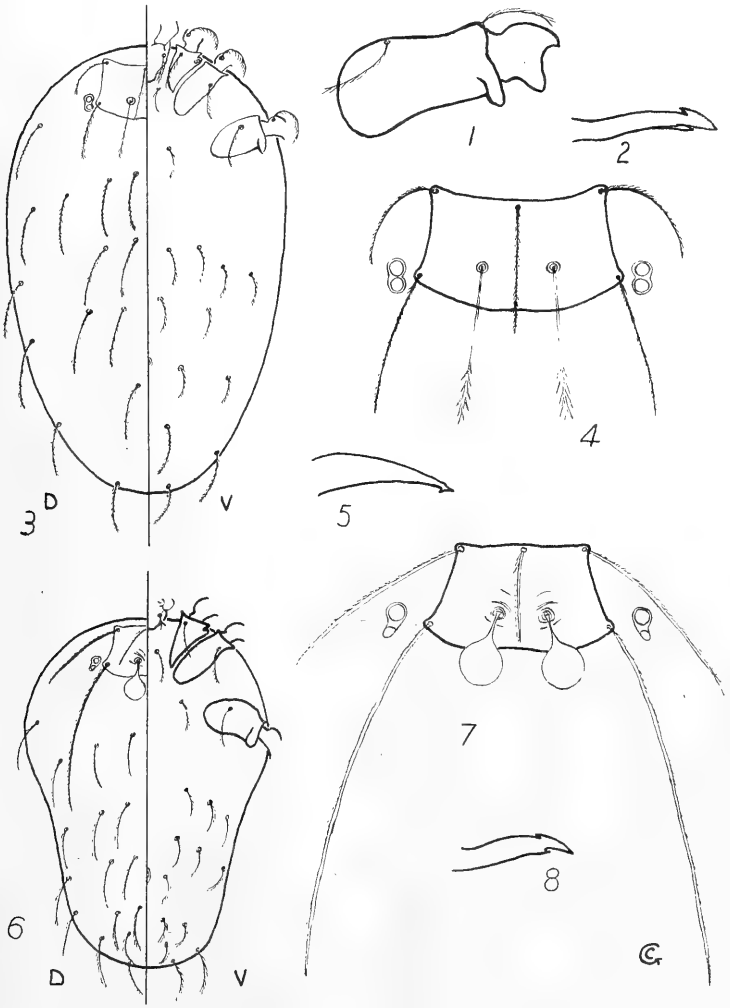


Fig. 1.—Coxa iii of *Paraschöngastia yeomansi.*

Fig. 2.—Chelicera of *P. retrocincta.*

Figs. 3-5.—*Trombicula vanderghinstei,* n. sp. 3, Composite dorsal and ventral diagram; 4, Scutum; 5, Chelicera.

Figs. 6-8.—*Neoschöngastia womersleyi,* n. sp. 7, Scutum; 8, Chelicera.

sides; length, 50μ; width, 84·4μ; set on the forward slope of the body, and only completely visible in newly-hatched specimens. Anterior margin concave; anterior corners angular, projecting slightly; lateral margins very slightly concave; posterior margin convex, the middle third straight or slightly concave; posterior corners angular and projecting slightly. Scutal setae 5: the AM* and PL straight, stout, with short branches on all sides; the AL curved, with short branches on the convex side only. The AM set back from the anterior margin, behind the AL; the AL and PL in the corners. AM, 50μ; AL, 46μ; PL, 56μ. Pseudostigmata two-thirds of the distance back, just in front of the PL setae; 28μ apart. Pseudostigmatic organs filiform, fine, straight, with 7 to 9 long fine branches on the distal two-fifths; length, 63μ. Ocular shield 6μ from the scutum, indented opposite the posterior corners. Eyes double, the anterior the larger and set opposite the pseudostigmata; the posterior just behind the PL setae. Body setae 54: of two forms—those of the dorsum and the last two rows of the venter stout, with short branches on all sides; the remainder of the venter shorter, finer, with relatively longer branches on the convex side only. Dorsum: setae 28, in rows as follows: 2, 8, 6, 6, 4, 2. Row 6 is on the posterior margin of the body. Venter: setae 26, in rows as follows: 2, 2, 8, 4, 4, /4, 2. Row 5 is at the level of the anus. Legs long: i, 209μ; ii, 165μ; iii, 228μ. Leg setae long, slender, slightly curved, with long fine branches on the convex side. Coxal setae single. The seta on each second segment very long and curved. Sixth segments and tarsi of legs i and ii short and wide, those of leg iii very long and slender. A very short stout spur on tarsi i and ii; no spur or nude seta on tarsus iii.

Principal host: The brown scrub rat (a local variant of *Rattus mordax* (*sensu lato*) Thomas 1904), colonies inside the ears. Casual host: Brown's rat (*R. browni* Alston 1877).

Taken at Bulolo, T.N.G., October, 1939. Type specimen in the collections of the School of Public Health and Tropical Medicine, University of Sydney.

This mite belongs to the closely-related group containing *T. minor*, *T. akamushi*, *T. deliensis*, *T. pseudoakamushi* Tanaka 1916, and *T. wichmanni*. Much of the confusion which previously existed in this group has been cleared up, now that Womersley (1939) has proved that *T. hirsti* (and therefore *T. pseudoakamushi* Hatori 1918) is identical with *T. minor*. *T. vanderghinstei* is probably only a local variant of *T. deliensis*, but it is described here as a distinct species until further details about the latter (and the true relationship between *T. deliensis* and *T. akamushi*) can be obtained. They differ in the following respects:

	T. deliensis	*T. vanderghinstei*
Maxillary setae:	nude	branched
Setae on palpal segment iii:	1 nude	1 nude, 1 branched
Scutum:	37μ × 74μ	50μ × 84·4μ

The number and arrangement of the body setae definitely distinguish *T. vanderghinstei* from *T. akamushi*.

Genus NEOSCHÖNGASTIA Ewing 1929.

Manual External Parasites, 187.

NEOSCHÖNGASTIA WOMERSLEYI, n. sp. Figs. 6, 7, 8.

Body piriform, widest at level of coxae iii, narrowing sharply just behind them; the posterior pole rounded. Striations moderately strong and fine. Pitting on

* As in previous papers, AL = anterolateral, AM = anteromedian, and PL = posterolateral.

scutum, maxilla, and coxae. Colour pale orange-yellow. Length, 275μ; width, 192μ; largest seen, 320μ × 223μ. Cephalothorax relatively very small. Maxillary setae very short, stout, with two branches. Chelicerae short, stout, slightly curved, tapering to a sharp point. Dorsoapical tooth a fine sharp backward-pointing barb; ventral tooth opposite it, prominent, pointing forward. A long fine nude seta on each cheliceral sheath. Palpi short, rounded, stout at the base, tapering sharply. Details of setae very hard to see. A short seta with several fine branches on ii; a short seta with two branches on iii; on iv, setae approximately as follows: one, stout, with long branches, and one, nude, at the base; two, nude, half-way; one, nude, at the apex; and one with many branches between the previous two. Appendiculum very small, rounded, bearing one short nude seta at the base and four long straight stout setae with long branches along one side. Palpal claw trifurcate, the central element straight, sharp, and tapering roundly; the ventral and dorsal elements shorter, straight, sharply pointed. Scutum twice as wide as long, the anterior margin two-thirds as long as the posterior; length, 39μ; width, 75μ. Anterior margin almost straight; anterior corners angular and projecting slightly; lateral margins concave; posterior margin convex, the middle third concave; posterior corners angular and projecting. Scutal setae 5: the lateral setae long, stout, and slightly curved, bearing a very few fine short branches on the convex side; the AM shorter and finer, with more and larger branches. The AM on the anterior margin; AL in the anterior corners, in line with the AM; PL in the posterior corners. AM, 36μ; AL, 60 to 80μ; PL, 120 to 150μ. Pseudostigmata two-thirds of the way back, just in front of the PL setae; 19μ apart. Crest represented by short oblique lines in front of and behind the pseudostigmata. Pseudostigmatic organs capitate, circular, with no apparent setules; length, 30μ; head, 18·8μ × 16·6μ; stem, 11·2μ. Ocular shield 7·5μ from the scutum. Eyes double, the anterior much the larger, opposite the pseudostigmata; the posterior behind the PL setae. Body setae 56(58), of two forms: those of the dorsum and the last row of the venter short, with short branches on the convex side; the remainder of the venter shorter and finer, with longer branches. Dorsum: setae 28, arranged in rows as follows: 2, 6, 6, 6, 2(4), 4(2), 2. Row 5 has its setae on the lateral margins of the body, in line behind row 1; row 7 is on the posterior margin of the body. Venter: setae 28(30), in rows as follows: 2, 2, 6, 6, 2, 4(6), 2, /4. Row 5 is at the level of the anus; row 8 is on the posterior margin of the body. Legs relatively long; i, 209μ; ii, 167μ; iii, 222μ. Leg setae with short branches on the convex side. Coxal setae single. Sixth segments not markedly expanded or constricted. A short spur on tarsi i and ii; neither spur nor nude seta on iii.

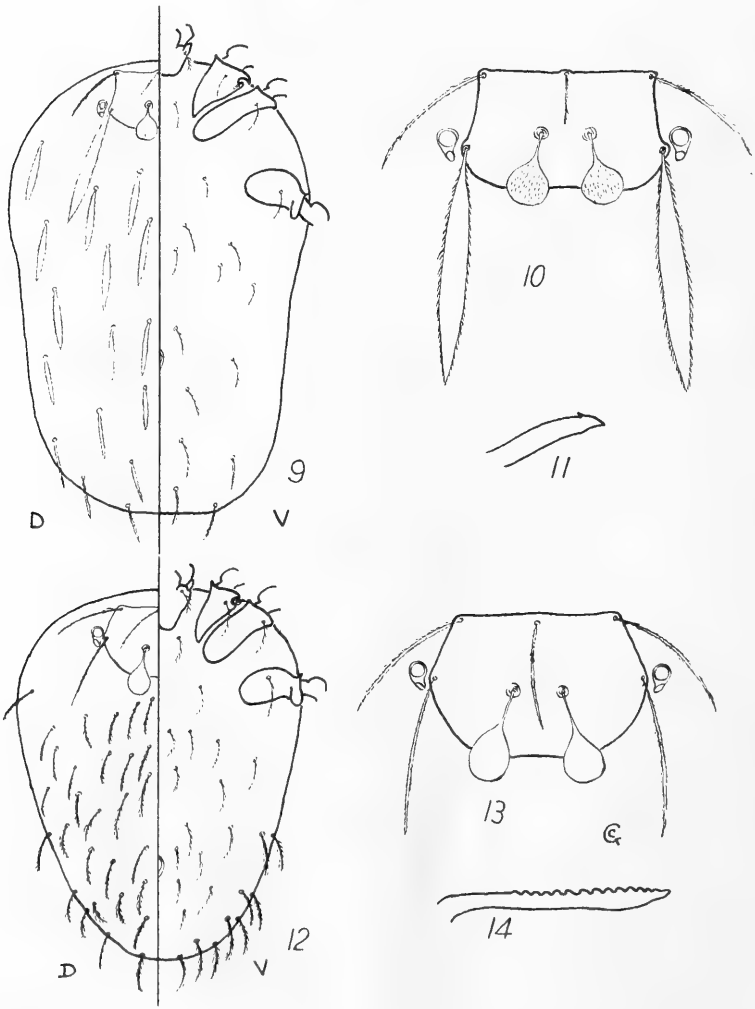
Principal host: Scrub wallaby (a local highland form of *Macropus* (*Thylogale*) *coxeni* Gray 1866), colonies inside the ears. Taken at Bulolo, T.N.G., November, 1939.

Type specimen in the collections of the School of Public Health and Tropical Medicine, University of Sydney.

NEOSCHÖNGASTIA FOLIATA, n. sp. Figs. 9, 10, 11.

Body oval, widest at level of coxae iii, and narrowing very slightly just behind them; the posterior pole bluntly rounded. Striations very fine. Pitting on scutum, maxilla, and coxae. Colour pale orange-yellow. Length, 358μ; width, 240μ; newly-hatched, 187μ × 131μ; largest seen, 389μ × 278μ. Maxillary setae stout, with about six fine branches. Chelicerae slender, slightly curved, tapering bluntly to a sharp point. Dorsoapical tooth a fine sharp barb. Ventral tooth a slight smooth swelling. A long slender nude seta on each cheliceral sheath.

Palpi short and angular. A fine seta with many branches on ii; a shorter seta with a few branches on iii; on iv, one branched seta at the base and two, nude, half-way. Appendiculum very small, bluntly pointed, bearing one short stout nude seta at the base and four branched setae, one very long and stout. Palpal claw trifurcate, the central element the longest, the ventral the shortest. Scutum well forward, almost twice as wide as long; length, 47μ; width, 84μ. Anterior margin straight, projecting around the AM seta; anterior corners rounded, projecting slightly; lateral margins concave; posterior margin convex, curving forward in the lateral fifths to meet the posterior corners; posterior corners rounded. Scutal setae 5: the AM very short and fine, with fine branches all over; the AL longer and stouter, with branches on all sides; the PL broad and



Figs. 9-11.—*Neoschöngastia foliata*, n. sp. 10, Scutum; 11, Chelicera.
Figs. 12-14.—*Schöngastia taylori*, n. sp. 13, Scutum; 14, Chelicera.

flat, very long, conforming to the type of the dorsal body setae. The AM in the projection of the anterior margin, in line with the AL; the lateral setae in the corners. Their lengths vary, sometimes even on the same specimen: AM, 19 to 25μ; AL, 50 to 56μ; PL, 87 to 100μ. Pseudostigmata just more than half-way back, in front of the PL setae; 19μ apart. No obvious crest. Pseudostigmatic organs capitate, the head circular and covered with fine short setules; length, 28μ; head, 15μ × 16μ; stem, 13μ. Ocular shield very close to the scutum. Eyes double, the anterior the larger, opposite the pseudostigmata; the posterior behind the PL setae. Body setae 60: those of the dorsum flat, narrow at the base, 6·5μ wide at the middle, 50 to 62·5μ long, tapering to a sharp point, with two rows of short setae down each edge. Those of the venter very short and fine, slightly curved, with short fine branches on the convex side; towards the posterior pole they are longer and thicker. Dorsum: setae 32, arranged in rows as follows: 2, 6, 6, 6, 6, 4, 2. Row 7 is on the posterior margin of the body. Venter: setae 28, arranged in rows as follows: 2, 2, 4, 6, 4, 2, 4, 4. The anus is between rows 5 and 6; row 8 is on the posterior margin of the body. Legs short: i, 182μ; ii, 155μ; iii, 215μ. Leg setae fine, short, slightly curved, with short branches on the convex side. Coxal setae single. A short stout spur on tarsi i and ii.

Principal host: Scrub wallaby (a local highland form of *Macropus* (*Thylogale*) *coxeni* Gray 1866), colonies inside the ears. Taken at Bulolo, T.N.G., November, 1939.

Type specimen in the collections of the School of Public Health and Tropical Medicine, University of Sydney.

Genus Schöngastia Oudemans 1910.

Ent. Bericht., iii, No. 54, 86.

Schöngastia taylori, n. sp. Figs. 12, 13, 14.

Body oval, widest between coxae ii and iii, posterior pole narrow. Striations fine and strong. Pitting on scutum, maxilla, and coxae. Colour bright orange. Length 292μ; width, 223μ; newly-hatched, 209μ × 125μ. Maxillary setae short, with about 7 branches. Chelicerae long and slender, armed with 14 denticles along the distal four-fifths. Cheliceral sheaths as long as the chelicerae, each bearing a long slender nude seta. Palpi rounded; a short branched seta on ii and iii; on iv, one seta with about four branches near the base, and one, nude, near the apex. Appendiculum rounded, bearing two nude and four branched setae. Palpal claw bifurcate, the medial element long, stout, and hooked, the lateral straight, shorter, and finer. Scutum rounded, roughly hexagonal, half as wide again as long; length, 57μ; width, 87μ. Anterior margin straight; anterior corners rounded; lateral margins straight; posterior margin convex, the middle third straight, the lateral thirds sloping forward to meet the posterior corners; posterior corners rounded. Scutal setae 5: stout, with many fine branches on all sides. AM back from the anterior margin, behind the AL setae; the lateral setae in the corners. Lengths varying: AM, 42μ; AL, 56μ; PL, 63μ. Pseudostigmata two-thirds of the way back, behind the PL setae; 19μ apart. Pseudostigmatic organs capitate, racquet-shaped, bearing no setules; length, 37·5μ; head, 23μ × 15μ; stem, 14μ. Ocular shield close to scutum. Eyes double, the anterior the larger, its posterior margin opposite the PL setae; the posterior opposite the pseudostigmata. Body setae 108; those of the dorsum stout, with short branches all over; those of the venter finer, with branches on the convex side only. Towards the posterior pole the dorsal rows continue around the sides of the body, the end setae encroaching

on the venter. Dorsum: setae 78, arranged in rows as follows: 2, 10, 2, 12, 2, 14, 2, 10, 12, 8, 4. Rows 3, 5 and 7 are on the lateral margin of the body, in line behind row 1; in some specimens these setae appear to be a continuation of the row next in front. Rows 6, 8, 9 and 10 each pass onto the venter. The setae of row 11 form a square on the end of the body. Venter: setae 30, arranged in rows as follows: 2, 2, 8, 4, 4, 4, 4, 2. The anus is between rows 6 and 7; rows 5, 7, and 8 are opposite the ends of dorsal rows, 6, 8, and 9 respectively. Legs long: i, 223μ; ii, 167μ; iii, 220μ. Leg setae fine, slightly curved, with branches on the convex side. Coxal setae single. Sixth segment of leg iii moderately constricted at the base, moderately expanded distally. Tarsi i and ii short and tapered; iii slender. A short stout spur on i; that on ii shorter and finer; a long slender nude seta on iii.

Principal host: Scrub wallaby (a local highland form of *Macropus* (*Thylogale*) *coxeni* Gray 1866), colonies on scrotum and hind legs. Taken at Bulolo, T.N.G., November, 1939.

Type specimen in the collections of the School of Public Health and Tropical Medicine, University of Sydney.

Acknowledgements.

My sincere thanks are due to Mr. F. H. Taylor, of the School of Public Health and Tropical Medicine, University of Sydney, who checked this paper and its references; and to Mr. E. Le G. Troughton, of the Australian Museum, who identified the hosts.

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AN EMPUSA ON A MITE.

By T. Petch.
(*Communicated by Dr. A. J. Nicholson.*)

[Read 26th June, 1940.]

In C.S.I.R. Pamphlet No. 84, "A population study of the red-legged earth mite (*Halotydeus destructor*) in Western Australia", etc.,* the author, Mr. K. R. Norris, recorded the occurrence of a fungus, a species of *Empusa*, on that pest. Subsequently, Mr. Norris kindly sent me specimens of diseased mites, and from these it was possible to confirm his identification. The field observations recorded below have been taken from Mr. Norris's data.

The mite normally has a jet-black body and red legs. When attacked by the fungus, the whole of the dorsal surface and the sides of the body are coloured yellowish-brown, and this area is sharply demarcated from the black ventral surface. Thus it is possible to pick out diseased mites in the field. Mr. Norris found that the change of colour was due to the presence immediately below the cuticle of a mass of hyphal bodies.

Individuals of *Halotydeus destructor*, killed by this *Empusa*, are attached to the host plant by their mouth parts, or are entangled in the tomentum of the leaf. There are no rhizoids. The conidiophores are short, stout and unbranched. The primary conidia are oval, 9–12 × 5–7μ, or subglobose, 8 × 6μ, in each case with a broad, truncato-convex papilla. The secondary conidia are similar, and are borne on a stout germ tube from any part of the primary conidium, but usually laterally, in the same manner as in *Entomophthora Aphidis*. As far as I am aware, no *Empusa* has been recorded previously on Acarina, and the present species does not agree with any known form. It is apparently a new species, which I name *Empusa acaricida*.

Empusa acaricida Petch, n. sp.

Conidiophoris brevibus, crassis, simplicibus; conidiis primariis ovalibus, 9–12 × 5–7μ, vel subglobosis, 8 × 6μ, conidiis secundariis similibus, papilla lata, truncato-convexa; hyphis rhizoideis nullis. On the earth mite, *Halotydeus destructor* (Acarina), Western Australia.

Changes of colour in insects attacked by species of Entomophthoraceae have rarely been recorded. Thaxter, in his *Entomophthoreae of the United States*, stated, concerning *Entomophthora Aphidis* (p. 177): "The conidiophores are white in the mass, often tinged with yellowish or flesh color from the coloring matter of the host, which usually assumes a pale brick red tint at or just before death. This change of color is, however, common to most aphides attacked by Empusae, and cannot be considered distinctive of any species." I have not observed that change of colour regularly in the numerous examples of these fungi on aphids which I have collected, except in the case of *Empusa Planchoniana* (Cornu) Petch.

* *H. destructor*, and no doubt also the *Empusa* which attacks it, has a very wide range in Australia, and occurs in many places in the Eastern States as well as in Western Australia.—Ed.

The latter species was described by Cornu from specimens on a black aphis, which was turned brick-red by the fungus. I have found it on a green aphis, on greengage, the insects again being turned red by the fungus; and Phillips described apparently the same species on *Aphis rumicis*, a black aphis, as *Entomophthora ferruginea*, the name being chosen because of the colour of the insect and the fungus. It would seem, therefore, that this colour change is usual in attacks of *Empusa Planchoniana* on aphids.

In flies, especially Syrphids, attacked by *Empusa Muscae*, the abdomen becomes enormously swollen, and appears white, with transverse black or grey lines. This colour, however, is a mechanical effect, due to the extension of the intersegmental membranes, so that the white internal fungus is seen through them.

How long the earth mite, *Halotydeus destructor*, can live after infection can only be determined by experiment, but Mr. Norris has furnished the following data bearing on the point:

One diseased mite collected 30th May died 3rd June
One diseased mite collected 30th or 31st May died 4th June
One diseased mite collected 31st May died 3rd June
One diseased mite collected 31st May died 8th June
Two diseased mites collected 1st June died 3rd June
One diseased mite collected 15th June died 23rd June
One diseased mite collected 15th June died 4th July

In all the foregoing instances, the dead mites produced conidia of the *Empusa*.

In general, insects attacked by Entomophthoraceae produce conidiophores and conidia shortly after death, unless dry weather conditions have set in, when the insect may dry up and a growth of *Cladosporium* or some allied fungus may supervene.

From the foregoing data, it appears that mites attacked by *Empusa acaricida* may be recognized by the change in their coloration at least nineteen days before they die. There is very little information on this point with regard to insects in general. Thaxter (*op. cit.*, p. 152) wrote, respecting Entomophthoraceae: "The period which ensues after the infection of a host until death varies to some extent. In the larger hosts, such as flies and caterpillars, death may not take place for twelve days; although the usual period is from five to eight days. In minute hosts, the period must be considerably shortened, owing to the ephemeral character of many of the forms known to be subject to the attack of Empusae."

The flies attacked by *Empusa Muscae*, noted above, in which the abdomen is abnormally swollen, are able to fly about until shortly before death, but it is not known how long they can retain their activity in that condition, as they have only been observed when they settled down for the last time, death ensuing in a few hours. With regard to fungi other than Entomophthoraceae, it may be recalled that Torrubia, who first described the "Vegetable Wasp", i.e. wasps attacked by *Cordyceps sphecocephala*, illustrated the insects flying about with the *Cordyceps* attached to them. That has been regarded as a traveller's tale, but a bee, bearing apparently the conidial stage of that fungus, has been caught flying about in England. The latter specimen is illustrated in Cooke's *Vegetable Wasps and Plant Worms*, fig. 12.

Although insects attacked by entomogenous fungi ultimately succumb to the attack of the parasite, it would appear from the few available records that they may continue their activities without being seriously incommoded for a longer period than would be expected.

NOTES ON AUSTRALIAN DIPTERA. XXXVIII.

FAMILY CHLOROPIDAE, Part ii.*

By JOHN R. MALLOCH.
(*Communicated by Frank H. Taylor, F.R.E.S., F.Z.S.*)

(Twenty-six Text-figures.)

[Read 26th June, 1940.]

Subfamily Oscinosominae.

I have already published a preliminary key to the genera of this subfamily in this series of papers, but in the key given below there are a number of genera included that were unknown to me as occurring in Australia when I wrote my previous key and I therefore present the new synopsis.

Key to the Genera.

1. Hind femur with spinose armature on ventral surface 2
   Hind femur without spinose ventral armature 3
2. Hind femur with a large triangular tooth or process near the apex on the antero-ventral surface; mesopleura haired in part ..... *Merodonta*, n. gen.
   Hind femur with a series of minute spinules on ventral surface ..... *Prionoscelus* Becker
3. Mesopleura with some quite long erect hairs on part of its upper posterior surface. 4
   Mesopleura either dusted or slightly pubescent, not distinctly haired 6
4. Hind tibia with a distinct apical ventral spur ..... *Lasiopleura*, subgen. *Terraeregina* Malloch
   Hind tibia without an apical ventral spur 5
5. Scutellum rounded in outline, the apical edge thick, without setigerous marginal warts ..... *Batrachomyia* Skuse
   Scutellum elongate, the apex thin, with several setigerous warts .. *Macrostyla* Lioy
6. Third antennal segment angular at apex ..... *Scoliophthalmus* Becker
   Third antennal segment disc-like, broadly rounded at apex 6*a*
6*a*. Fifth wing-vein absolutely straight along the discal cell 7
   Fifth vein with a more or less distinct flexure or weak part near middle of discal cell 9
7. Second wing-vein very short, ending in the costa close to apex of first vein, second section of the costa not half as long as third ..... *Siphunculina* Rondani
   Second wing-vein not exceptionally short, ending in the costa far from apex of first, the second section of costa at least as long as third 8
8. Scutellum about twice as long as its basal width, gradually tapered from base to apex, where it is about one-fourth as wide as at its base, with a broad shallow central sulcus; mesonotum trisulcate; hind tibial apical ventral spur large ..... *Euhippelates* Malloch
   Scutellum not longer than its basal width, rounded in outline, not centrally sulcate; hind tibial apical ventral spur microscopic ..... *Platyina* Malloch
9. Humeri each with two quite long bristles, the upper one on each incurved, the lower one backwardly directed; dorsocentral bristles on mesonotum usually quite long and more than two postsutural pairs present 10

* Continued from These PROCEEDINGS, lxiii, 1938, 334.

Humeri with but one bristle each, the upper inwardly-directed one lacking, or if it is present there are but two pairs of postsutural dorsocentral bristles 11

10. Arista normal in form in both sexes; hind tibia nearly always with a more or less evident apical ventral spur or bristle, sometimes very small; scutellum with two or more fine erect discal hairs in addition to the marginal bristles .... *Lasiopleura* Becker

Arista normal in form in the male, with the second segment much elongated and almost as long as the third in the male, in that sex geniculated between these segments; hind tibia without an evident apical ventral spur; scutellum without discal hairs, with only the marginal bristles ..... *Ephydroscinis* Malloch

11. Mesonotum with two pairs of long dorsocentral bristles, the anterior pair close to the suture; ocellar bristles long, proclinate and divergent .. *Oscinelloides*, n. gen.

Mesonotum with three pairs of dorsocentral bristles ..... *Genus novum**

Mesonotum with but one distinct pair of dorsocentral bristles 12

12. Hind tibia with a more or less well developed apical ventral spur .. *Cadrema* Walker

Hind tibia without an apical ventral spur 13

13. Frons flattened and precipitous from above middle to bases of antennae, the posterior third horizontal, the triangle not extending beyond the horizontal part; antennae situated well below middle of eye in profile; notopleural bristles 1 + 1 .... *Benjaminella* Malloch

Frons horizontal, or evenly descending to anterior margin; antennae usually inserted at or above middle of eye in profile; notopleurals variable in number 14

14. Scutellum much longer than its basal width, flattened above, tapered to apex, the sides straight, with a number of strongly setigerous warts on margin apically; mesopleura tomentose on upper posterior angle ..... *Thyridula* Becker

Scutellum not noticeably longer than its basal width, or markedly tapered to apex, sides not entirely straight or with marked setigerous warts 15

15. Face sharply carinate in centre, the anterior outline of epistome seen from below in the form of a wide V; penultimate section of fourth vein fully six times as long as penultimate section of third; frontal triangle well defined .... *Deltastoma* Malloch

Face with or without a central carina, but in all cases with the outline of the epistome seen from below forming a transverse or arcuate outline 16

16. Frontal triangle not defined beyond the immediate area of the ocelli; scutellum rounded in outline or flattened above and slightly tapered to apex where it is almost transverse and furnished with two short stiff bristles, the disc with stiff spinules; face deeply concave in profile ..... *Caviceps* Malloch

Frontal triangle usually well defined, always extending distinctly beyond the ocellar orbit, or the scutellum and face not as above 17

17. Thoracic dorsum with three deeply-punctate sulci, the central one usually a mere line, the others broader, particularly behind ..... *Tricimba* Lioy

Thoracic dorsum without three distinct sulci, sometimes with shallow foveae on the posterior dorsocentral lines that are more or less evidently punctate 18

18. Vibrissal angle very markedly produced, and the proboscis slender, heavily chitinized, geniculated in middle, either section as long as or longer than the lower margin of the head ..... *Madiza* Fallén

Vibrissal angle not markedly produced, if moderately so the proboscis is stout, not sharply geniculated, and at least the apical section is much shorter than lower margin of the head 19

19. Frontal triangle poorly limited, entirely or almost entirely thickly grey-dusted, usually very short, occasionally with a narrow grey line carried to anterior margin; thorax entirely black, either rather distinctly grey-dusted or with distinct quite dense piliferous punctures indiscriminately arranged on its entire dorsal surface and on the scutellum 20

Frontal triangle sharply limited, usually entirely glossy, or very faintly grey-dusted, or the dorsum of thorax and scutellum not densely piliferous punctate, or the general colour yellow, or partly black and yellow; if the thorax is entirely black the mesonotum is either glossy, or if thinly dusted then the hairs are in rather widely separated longitudinal series 21

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* I strongly suspect that *Oscinis cinerea* de Meijere, which I place at this point in my key, will require to be removed to a new genus, but lacking specimens I do not care to erect a new genus for its reception at this time. The species occurs in New Guinea and probably will be found in northern Australia.

20. Gena about one-third as high as eye; parafacial widely visible in profile; scutellum with a shallow depression along each side of disc ..... *Lipara* Meigen
Gena much less than one-third as high as eye; parafacial at most narrowly visible in profile; scutellum without depressions on sides of disc .... *Conioscinella* Duda
21. Mesonotum microscopically shagreened or granulose on surface, with the fine short hairs arranged in rather widely separated longitudinal series .. *Oscinella* Becker
Mesonotum not shagreened or granulose, shiny to glossy, the hairs longer and more numerous, not arranged in definite well-spaced longitudinal series 22
22. Triangle entirely glossy, more than half the length of frons and well defined, or yellow with a small black ocellar spot ..... *Lioscinella* Duda
Triangle usually merely shiny, not half as long as the frons and poorly defined ..... *Botanobia* Lioy

It should be noted that in making generic assignments of the Australian species I have carefully considered the characters of these and the genotypes. In a number of cases species have heretofore been placed in genera other than those to which they are now referred, but these are now, I hope, to be found in their proper places.

The genus *Gaurax* Loew, to which a few Australian species have been referred, does not occur on this continent.

This paper is intended merely as a supplement to my previous papers on the group, and as an aid to Australian students.

Merodonta, n. gen.

This genus, as noted above, may be at once distinguished from all others of the subfamily yet met with in Australia by the prominent subtriangular tooth or process near the apex of the anteroventral edge of the hind femur. A similar tooth occurs on the hind femur in a few genera of other families such as Syrphidae. The hind femur is much thicker than the other pairs, the hind tibia is curved so as to fit against the underside of the femur, and the posterodorsal surface has an elongate depressed area that tapers to a point at each extremity, but the depression is glossy and lacks the short pile characteristic of most genera in this subfamily, thus being more like the depression on the hind tibia of the males of certain Sepsidae or of some males of the genus *Dolichopus* Meigen. In other respects the new genus is quite similar to typical *Oscinosoma* except that there are some hairs on the upper posterior portion of the mesopleura as in *Dasyopa* Malloch.

Genotype, *Merodonta crassifemur*, n. sp.

Merodonta crassifemur, n. sp. Fig. 1.

♀. Occiput and ocellar region black, the remainder of head except the dark centre of face reddish-yellow, antennae of the latter colour, palpi testaceous-yellow. Frons fully two-fifths of the head-width, triangle not very well defined, fading out near middle of frons, bare, minutely shagreened or dusted; vertical, postvertical, and ocellar bristles distinct, some setulose hairs in a series along each orbit, stronger above, the interfrontalia with fine short hairs. The head is greasy so that it is impossible to determine if some dark spots near the anterior margin of the frons are or are not due to discoloration. Eyes much higher than long, sparsely short-haired; gena about one-eighth as high as eye and not equal to width of the short, very broadly apically rounded third antennal segment; vibrissal angle not produced, the hair fine but distinct; arista with the pubescence about as long as its basal diameter; proboscis short and thick; palpi normal. Thorax black, almost glossy, undusted, brownish round the humeral suture, lateral mesonotal margins, and the sutures of the pleura, and merging into brown at apex of scutellum. Mesonotum with rather dense small piliferous punctures, densest in the two broad

shallow postsutural dorsocentral depressions; the bristling as follows: 1 humeral, 1 + 2 notopleurals, 2 postalars, and 1 pair of dorsocentals. Scutellum semicircular in outline, convex on disc, with two long and two short marginal bristles, and numerous short discal hairs. Legs testaceous-yellow, all coxae brown, femora of fore and mid pairs black except their extremities, hind pair entirely black, mid tibiae darkened centrally, hind pair black except at bases. In addition to the preapical process on the hind femur there is a slight elevation of the ventral surface near middle (Fig. 1) that is transversely finely striate. Hind tibia without an apical spine; apical ventral spur on mid tibia well developed, straight. Abdomen tapered to apex, black and shiny on the sclerotized plates, the membrane brown. Hairs pale. Wings greyish-hyaline, veins pale brown. First and second sections of costa subequal in length, second about 1·5 times as long as third; penultimate section of third vein not more than half as long as penultimate section of fourth, the latter about one-fifth as long as its ultimate section; outer cross-vein oblique, about half as long as ultimate section of fifth vein; veins 3 and 4 slightly divergent apically, the latter ending behind the apex of the wing. Halteres yellow. Length, 3 mm.

Type, Townsville, Queensland (G. F. Hill).

Batrachomyia Skuse.

Proc. Linn. Soc. New South Wales, xiv, 1889, 174.

I have been unable to satisfy myself that either of the two species originally included in this genus has been seen by me and an examination of the type-specimens, if such are still available, will be necessary to ensure their identification.

Below I present a revised key to the species known to me.

Key to the Species.

1. Thoracic dorsum reddish-yellow, with four deep black vittae 2
   Thoracic dorsum brownish or reddish-yellow, with at most very faint reddish vittae 3
2. Notopleural area and the scutellum not much paler than the remainder of the thoracic dorsum, the scutellum not blackened on the lateral basal angles; humeri without a black spot; tibiae largely infuscated ..... *major* Malloch
   Notopleural area and the scutellum ivory-white, the latter blackened on the lateral basal angles; humeri with a black spot; tibiae entirely fulvous-yellow ..... *strigipes* Malloch
3. Third antennal segment entirely fulvous-yellow; femora entirely yellow-haired ..... *flavicornis* Malloch
   Third antennal segment deep black; femora not entirely yellow-haired 4
4. Legs entirely fulvous-yellow 5
   Legs fulvous-yellow, with the following parts black: apices of femora narrowly, fore and mid tibiae, except the mid pair which are faintly yellowish centrally, the extremities of hind tibiae, and the entire tarsi ..... *varipes*, n. sp.
5. Notopleural and marginal scutellar bristles not, or but slightly, differentiated from the long erect black hairs; mesopleura with some long stiff black hairs amongst the finer pale hairs; genae with some dark hairs on vibrissal angles; the black spot on ocellar region extending well in front of and behind the orbit of the ocelli ..... *atricornis* Malloch
   Notopleural and marginal scutellar bristles well developed, distinct from the adjacent much shorter black hairs; mesopleura entirely yellowish-white-haired; genae entirely yellow-haired; the black spot on ocellar region hardly extending outside of the ocellar orbit ..... *dubia*, n. sp.

Batrachomyia varipes, n. sp.

Head orange-yellow, a spot enclosing the ocelli, apex of second and all of the third antennal segment, and the aristae, deep black; palpi yellow. Frons a little

longer than wide, quite densely furnished with short black hairs. Eyes with dense pale fine hairs. Genae at middle about as high as width of the third antennal segment, the latter higher than long, broadly rounded at its apex; genal hairs mostly yellow. Thorax orange-yellow or fulvous-yellow, the mesonotum with faint traces of four reddish vittae, but the specimen has evidently been in liquid, so the colour markings are not very clear. Surface mostly abraded, but the hind margin of the mesonotum has some quite long black hairs, and the scutellar hairs that remain are also black. Legs coloured as thorax, the apices of all the femora narrowly black, the fore and mid tibiae black, the mid pair faintly yellowish centrally on dorsum, the middle of the hind tibiae broadly yellow, their extremities black, and all the tarsi black. Wings hyaline, veins brown. Halteres with yellow knobs. Abdomen fulvous-yellow. Length, 6 mm.

Type, Mallee, Victoria (Coll. Lichtwardt, Deutsches Entomologisches Institut).

BATRACHOMYIA DUBIA, n. sp.

♀. Similar in general colour and structure to *atricornis*, differing in the characters listed in the foregoing key to the species. The black spot on the ocelli extends very slightly behind the posterior level, but not beyond the limits of the ocellar orbit elsewhere, while in *atricornis* it is much larger, elongate triangular, and extends well in front of and behind the orbit of the ocelli. The genae are entirely yellow-haired, and the hairs are finer in front than in *atricornis*. The mesopleural hairs are also much finer than the darker hairs in the other species, while there is a variable number of well-developed notopleural bristles, and on the apical margin below there are a number of black bristles or strong bristly hairs that are much longer than the short erect fine discal black hairs. Length, 6–7 mm.

Type, Upper Beaconsfield, Victoria, x.1930 (J. Evans). Paratype, Narooma, N.S.W., 25.xi.1930 (A. L. Tonnoir).

BATRACHOMYIA ATRICORNIS Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, 1, 1925, 336.

♂, ♀. Sydney, N.S.W., 14.ix.1924 (Health Dept.).

MACROSTYLA Lioy.

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

This genus, also known under the names *Meroscinis* de Meijere and *Rhodesiella* Adams, was not included in my key to the genera of this subfamily. It may be distinguished from closely-related genera by the lack of a sensory area on the hind tibia, and the presence of short but quite evident erect hairs on the mesopleura. In the only Australian species known to me the scutellum is about half as long as the mesonotum, but slightly convex above, coarsely piliferous-punctate on surface including the sides, thin at apex which is rounded and armed with four short warts, each of which has a quite strong bristle surmounting it, of which the apical two are the longer.

MACROSTYLA PUNCTIFRONS, n. sp. Figs. 2–4.

♂. General colour black, with a distinct blue-green metallic tinge, most marked on the frontal triangle, least so on the abdomen. Head in profile as Figure 2. Frontal triangle shiny blue-green, shaped as in Figure 3, along each side with about five rather large shallow punctures in each of which there is an inwardly-directed curved pale setule, and on the central line with three large shallow depres-

sions or punctures, the one in front of ocelli broad, the upper part microscopically striate, the remainder of surface less distinctly so. Frons laterad of the triangle dull brownish-black, with a series of pale hairs along eye-margin, and another, less developed, along triangle. Vertical bristles yellowish-white, inner verticals short, postverticals cruciate, ocellars weak. Face concave, bifoveolate, centrally greenish-black, laterally brown, epistome quite sharp and transverse; vibrissae white; parafacial and upper margin of gena white-dusted. Antennae brownish-yellow, third segment infuscated above and at apex; arista pale at base, fuscous beyond, entirely bare. Mouth parts destroyed in type. Occiput shiny black. Eyes bare. Thorax and scutellum entirely black, with a distinct blue-green tinge on the dorsum; mesonotum, scutellum, and mesopleura coarsely and closely piliferous-punctate, the hairs, anterior notopleural, and posterior marginal bristles on mesonotum yellowish-white, posterior notopleural and scutellar bristles black, no sulci on mesonotum. Scutellum longer than its basal width, the marginal warts longer than thick. Postscutellum forming a large convexity on underside of scutellum. Coxae, trochanters, knees narrowly, extreme apices of tibiae and basal

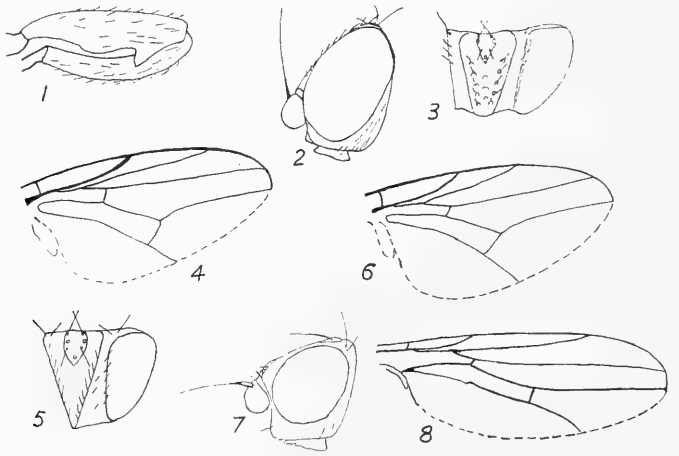


Fig. 1.—*Merodonta crassifemur*, n. sp. Hind femur-tibia.
Figs. 2-4.—*Macrostyla punctifrons*, n. sp. 2, Head in profile; 3, frontal triangle; 4, wing.
Figs. 5, 6.—*Macrostyla regina*, n. sp. 5, Head; 6, wing.
Figs. 7, 8.—*Oscinelloides bispinosa* (Becker). 7, Head; 8, wing.

four segments of tarsi, testaceous-yellow, remainder of legs black. Femora stout, the fore pair with a quite well developed series of bristly hairs from basal third to apex on postero-ventral surface; no short spinose armature on any femur. Wings whitish-hyaline, veins pale brown, yellowish basally. Venation as Figure 4. Abdomen with a blue-green tinge, tergites progressively more densely haired from second to fifth, the hairs black. Halteres missing in type specimen. Length, 3 mm.

Type, Palm Is., Qsld. (Mrs. F. H. Taylor).

The entirely bare, very slender, aristae and coarsely punctured frontal triangle are characters that distinguish this species from any other known to me. The bare arista is met with in only two other species, both African, in this genus so far as is now known to me.

MACROSTYLA REGINA, n. sp. Figs. 5–6.

♀. A glossy-black species, with a bluish tinge on frontal triangle and an aeneous shade on the abdomen. Legs black, trochanters, extreme apices of femora, apices of the tibiae and all of tarsi fulvous-yellow. Wings whitish-hyaline, veins yellow. Knobs of halteres brown. Head black, antennae yellowish-brown, palpi fuscous, sides of frons in front brownish, shiny, the triangle smooth and glossy, with some fine hairs along its sides and attaining almost to the anterior margin (Fig. 5). Vertical width of frons nearly one-half the head-width, sides straight, length about equal to width, about six rather long setulose hairs on each orbit, the vertical, postvertical and ocellar bristles well developed but not very strong. Eye fully 1·25 times as high as long; gena almost linear, dull brownish-black, with fine black lower marginal hairs that are longer at the very slightly produced vibrissal angle. Antennae moderate, third segment disc-like, arista distinctly pubescent, the longest hairs about as long as its basal diameter. Thorax glossy-black, without dusting. Mesonotum and scutellum closely and quite deeply piliferous-punctate, the hairs brown, bristles black. Notopleurals 1 + 2. Scutellum about two-thirds as long as mesonotum, and distinctly longer than its basal width, tapered evenly to the narrowly transverse apex, with two well-developed warts at apex on which there are bristles that are fully two-thirds as long as the scutellum, and on each side at apical third another lateral wart which bears a very short bristle. The single postalar bristle is quite strong and situated on a distinct wart. Legs rather stout. Fore femur without an anteroventral comb, with a series of moderately long fine posteroventral hairs that are yellowish basally and darker apically. Wing as Figure 6. Basal costal bristles both very short and fine. Abdomen broadly ovate, tapered at apex, genital lamellae slender. Length, 2 mm.

Type, Brisbane, Qsld., in house (Dr. A. J. Turner).

SIPHUNCULINA Rondani.

Dipt. Ital., Prod., i, 1856, 128.

I have nothing to add to what I have already published on this genus.

EUHIPPELATES Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, l, 1925, 96.

EUHIPPELATES PALLIDISETA Malloch.

Op. cit., l, 1925, 96.

Five specimens from Sydney, N.S.W., taken in September, October and January (Health Dept.).

PLATYINA Malloch.

Op. cit., lii, 1927, 436.

I have nothing to add to the published records of this genus.

BENJAMINELLA Malloch.

Op. cit., l, 1925, 336.

I have seen no additional specimens of the genotype and only species.

OSCINELLOIDES, n. gen.

This genus may be at once distinguished from related genera by the possession of two pairs of strong dorsocentral bristles, one near hind margin and the other close to the suture. The vertex has one long strong bristle on each side, the post-vertical pair of bristles are mere short hairs, and the ocellar bristles are quite

long, proclinate, and divergent (Fig. 7). This last character, as well as the rather narrow wings, appears to associate the genus with *Stenoscinis* Malloch (*Rhopaloptternum* Duda), an American and African genus. The only specimen that I have is damaged by the pin on which it is mounted, but I can detect one strong humeral, one notopleural, and a long fine hair on the upper margin of the sternopleura. The scutellum is short, with one pair of long apical bristles and a pair of very short fine lateral hairs. The frontal triangle is large and glossy, the antennae short, with rounded third segment, and the aristae are pubescent; genae narrow. The second and third segments of the costa are about equally long, the first posterior cell is slightly narrowed at apex, and the discal cell is almost equally wide from close to base to apex, with the inner cross-vein distinctly proximad of middle (Fig. 8).

Genotype, *Oscinella bispinosa* Becker.

Oscinelloides bispinosa (Becker). Figs. 7–8.

A small slender species superficially resembling certain species of Asteiidae, but distinguished at once by the lack of vibrissae, etc. The face is silvery-white-dusted, the frons in front and the antennae and palpi orange-yellow, remainder of frons black, the triangle glossy, thorax and abdomen glossy-black, legs brownish-yellow, mid and hind femora blackened apically, fore tibiae apically and fore tarsi browned.

Originally described from New Guinea. One female from Rabaul, N. Britain (F. H. Taylor).

There appears to be good reason to erect a genus for the reception of *Oscinis cinerea* de Meijere, as noted in footnote under the foregoing generic key, but probably there are many more species in Australia and New Guinea that should be similarly treated and only a careful consideration of a much larger collection than I have now in hand will definitely establish the relationships of even some of the species now dealt with in such generic concepts as *Lioscinella* and *Botanobia*.

Lasiopleura Becker.

Archiv. Zool. Budapest, i, 1910, 130.

As already pointed out by me, in Part xxxv of this series of papers (Proc. Linn. Soc. New South Wales, lxi, 1936, 23), this genus is the same concept as *Parahippelates* Becker. Below I present a key to the species at present known to me from Australia. All the species have the notopleurals 1 + 1.

Key to the Species.

1. Mesopleura with fine pale hairs on its entire surface (Subgenus *Terraeregina* Mall.) ..... *dasypleura* Malloch
   Mesopleura bare (Subgenus *Lasiopleura* Becker) 2
2. Wing with a large well-defined black or dark brown mark in centre or on costa .. 3
   Wing without a well-defined black or dark brown mark, at most with a linear brownish costal suffusion 5
3. Wing with an elongate dark-brown mark on the costa from about basal third of the second section to its apex that does not extend over third vein on disc; apical section of fifth vein subequal to preapical section of fourth; thorax shiny brownish-black, with slight brownish-grey dust ..... *costomaculata* Malloch
   Wing with a much larger black mark from a little beyond base of second costal section to its apex that extends over disc to fifth vein; apical section of fifth vein very much shorter than preapical section of fourth; thorax brownish-black, hardly shiny, with central portion of anterior half or more of the mesonotum and a large portion or all of the pleura densely white or yellowish-white dusted 4

4. Frons densely white-dusted on upper half or more, not at all shiny; mesonotum with a yellowish-white-dusted central vitta on anterior half or more that extends a little laterad of the dorsocentral bristles and is palest on lateral margins; femora broadly yellow at apices ..... *ornatipennis* Malloch

Frons less densely white-dusted on upper half, the latter black and rather distinctly shiny; mesonotum with a silvery-white-dusted vitta that does not entirely fill the area between the dorsocentral bristles and tapers off a little behind the suture; femora black, extreme apices yellowish ..... *exquisita*, n. sp.

5. Costal margin of the wing rather noticeably browned from apex of first vein to apex of fourth; dorsum of thorax fulvous-yellow, very distinctly shiny, with very faint dusting; third antennal segment largely brown; arista dark-haired, the longest hairs about as long as its basal diameter ..... *brunneicosta* Malloch

Wing hyaline or with very faint trace of yellowish on most of its extent; other characters not as above 6

6. Aristae white, with dense short white hairs; femora and tibiae largely or entirely blackened; halteres dark brown; wings hyaline, last section of fourth vein more than twice as long as preceding section; thorax dark fulvous, with distinct but not dense pale dusting ..... *albiseta* Malloch

Aristae and their hairs dark brown 7

7. Aristae plumose, the longest hairs as long as the width of the third antennal segment ..... *rufescens* Duda

Aristae much shorter haired, the longest hairs not more than half as long as width of the third antennal segment 8

8. Aristae short haired, densely so on basal half, the longest hairs at least twice as long as its basal diameter 9

Aristae almost bare, at most with pubescence which is not as long as its basal diameter, if more distinctly haired the hairs not twice as long as its basal diameter 12

9. Mesonotum dark brown, slightly shiny, with a broad central grey-dusted vitta that extends laterad of the dorsocentrals and is most distinct in front; scutellum not as noticeably grey-dusted, yellowish on margin; antennae entirely pale yellow ..... *griseovitta* Malloch, ♂

Mesonotum not coloured as above, without a broad central grey-dusted vitta 10

10. Pleura entirely reddish-yellow; longest hairs on aristae about half as long as the width of third antennal segment ..... *nigripila* Duda

Pleura not entirely reddish-yellow; longest hairs on aristae distinctly less than half as long as width of third antennal segment 11

11. Pleura and lateral margins of the mesonotum reddish-yellow, the sternopleura black below; mesonotum not shiny, and without distinct vittae; outer cross-vein of the wing almost twice its own length from apex of fifth ..... *duplicata* Malloch

Thorax black, propleura reddish-yellow, mesonotum shiny, distinctly vittate; outer cross-vein of the wing at a little more than its own length from apex of fifth ..... *aequalis* Becker

12. Gena very high, subequal in height to the eye; parafacial as wide as third antennal segment; a bright orange-yellow to fulvous-yellow species; the genal bristle very short; tibial spur not as long as diameter of tibia, but strong and slightly bent ..... *conopsea* Duda

Gena not nearly as high as eye, parafacial not more than half as wide as third antennal segment and the other characters not as above 15

13. Hind tibial spur indistinct, straight, very small and fine, and not nearly half as long as the tibial diameter, sometimes practically lacking; all presutural acrostichals minute 14

Hind tibial spur curved and stout, usually at least as long as the tibial diameter 15

14. Legs testaceous-yellow, only the apical two segments of the tarsi of mid and hind legs slightly darkened; fifth visible abdominal tergite and hypopygium of male yellow, the former with several rather fine long black downwardly-directed bristles on the sides; thorax with the dorsum evenly and densely coated with grey dust; a line drawn in continuation of the outer cross-vein to costa would pass through second vein close to its middle in male; presutural bristle strong ..... *seticauda* Malloch

Legs with at least the hind femora and tibiae largely fuscous; dorsum of the thorax glossy-black, with a purplish tinge, and two central faintly indicated whitish-dusted lines anteriorly; a line drawn in continuation of the outer cross-vein to the costa would pass through the apex of second vein; venation in the sexes different, the first posterior cell in the male much narrower basally than in the female; presutural bristle lacking ..... *anomala* Malloch

15. Mesonotum shiny reddish to dark brown, with a broad grey-dusted central stripe that extends outside of the lines of dorsocentrals; scutellum grey-dusted on disc; hind tibial spur about as long as diameter of the tibia; antennae very pale yellow ..... *griseovitta* Malloch, ♂

Mesonotum without a grey-dusted vitta covering the intradorsocentral area 16

16. Mesonotum with the acrostichals on the anterior half or more very short and fine, not decussate, biseriate; hind tibial spur not longer than the tibial diameter ..... *taylori*, n. sp.

Mesonotum with some of the acrostichals on the anterior half about half as long as the anterior dorsocentrals, and decussate; hind tibial spur longer than the tibial diameter 17

17. Gena almost as high as the eye; thorax entirely shiny black, with grey or brownish-grey dust, the mesonotum with faint dark vittae, the central linear dark brown one most distinct, especially posteriorly; hind tibial spur strong, much curved 20

Gena not or very little more than half as high as eye 18

18. Thorax shiny brownish-yellow, the mesonotum reddish-brown, with two grey-dusted vittae along the lines of dorsocentrals; third antennal segment largely fuscous ..... *griseovitta* Malloch, ♀

Thorax shiny black or brownish-black, the mesonotum faintly if at all vittate .. 19

19. Legs honey-yellow, all femora largely blackened centrally ..... *parva* Malloch

Legs entirely honey-yellow ..... *parva*, var. *pallipes*, novum

20. Legs entirely tawny-yellow; mesonotum with grey dust, only a central faint dark vitta showing, most distinct behind ..... *nudiseta* Becker

Legs honey-yellow, femora largely blackened; mesonotum with brownish dust and three quite distinct dark vittae ..... *fuscipes* Malloch

LASIOPLEURA (TERRAEREGINA) DASYPLEURA Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, liii, 1928, 303.

Known from only the type material. Queensland.

LASIOPLEURA (LASIOPLEURA) COSTOMACULATA Malloch.

Op. cit., xlix, 1924, 329.

Described from Sydney. I have seen an additional specimen from the same locality.

LASIOPLEURA (LASIOPLEURA) ORNATIPENNIS Malloch. Fig. 9.

Op. cit., xlviii, 1923, 620.

Described from Chelsea, V., the type-specimen a female. I have two additional female specimens from Collaroy, near Sydney, N.S.W., 24.i.1924 (E. W. Ferguson). Apex of hind tibia and spur as Figure 9.

LASIOPLEURA (LASIOPLEURA) EXQUISITA, n. sp. Fig. 10.

♀. Head black, face, genae except posteriorly, and anterior half of frons orange-yellow, the whole with changeable silvery-white dusting, most dense on the dark parts; antennae, aristae except bases, and the palpi, orange-yellow. Frons slightly depressed, at vertex two-thirds of the head-width, narrowed to anterior margin, as long as its vertical width. Inner vertical and the proclinate ocellar bristles long, outer vertical not half as long as inner and slightly shorter than the cruciate post-verticals, each orbit with about three pairs of short black setulae, and the inter-frontalia with two or three pairs of cruciate setulose hairs. Antennae rather small,

the arista bare, not twice as long as width of third antennal segment; parafacial about half as wide as third antennal segment; gena about two-thirds as high as eye, with some short black hairs on surface and a short black vibrissa; eye bare, longer than high; genal bristle minute. Thorax blackish-brown, mesonotum glossy, with a silvery-white-dusted vitta from anterior margin to just beyond the suture that does not overlap the dorsocentrals and is abruptly tapered to a point behind; pleura densely silvery-white-dusted except on upper edge; scutellum with a large silvery-white-dusted spot on each side. Bristling normal, presutural strong, presutural acrostichals minute, sparse; sternopleural present; a few short discal hairs on scutellum. Wing whitish-hyaline, veins dark brown, pale brown clouds in costal and anterior basal cells up to the furcation of second and third veins, and along the posterior side of fifth vein to its flexure; a large black mark on disc extending from near middle of second vein to its apex and back over disc to the fifth vein, filling apical half of discal, basal half of first posterior except extreme base, central third of submarginal, and base of second posterior cell. Fifth vein curved evenly down on penultimate section so that the discal cell is parallel-sided on apical two-thirds; ultimate section of fifth vein about half as long as penultimate section of fourth. Halteres whitish-yellow. Legs black, silvery-white-dusted, extreme apices of femora, all of tibiae and tarsi, orange-yellow, sometimes the middle of hind tibiae and apical two segments of tarsi slightly infuscated. Hind tarsi much longer than their tibiae; hind tibial spur minute, a mere setule (Fig. 10). Abdomen coloured as thorax, second (first visible) tergite, and a large spot on each side of third and fourth below the lateral curve silvery-white-dusted. Length, 3 mm.

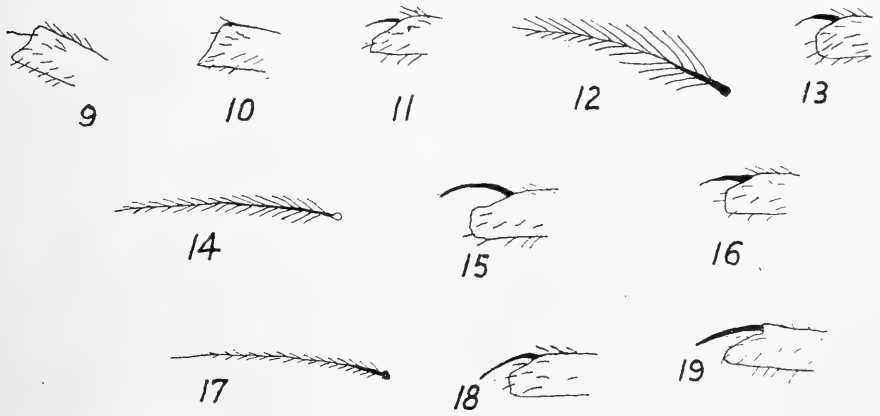


Fig. 9.—*Lasiopleura* (*Lasiopleura*) *ornatipennis* Malloch. Apex of hind tibia and spur.

Fig. 10.—*Lasiopleura* (*Lasiopleura*) *exquisita*, n. sp. Apex of hind tibia and spur.

Fig. 11.—*Lasiopleura* (*Lasiopleura*) *albiseta* Malloch. Apex of hind tibia and spur.

Fig. 12.—*Lasiopleura* (*Lasiopleura*) *rufescens* Duda. Arista.

Fig. 13.—*Lasiopleura* (*Lasiopleura*) *griseovitta* Malloch. Apex of hind tibia and spur.

Fig. 14.—*Lasiopleura* (*Lasiopleura*) *duplicata* Malloch. Arista.

Fig. 15.—*Lasiopleura* (*Lasiopleura*) *aequalis* Becker. Apex of hind tibia and spur.

Fig. 16.—*Lasiopleura* (*Lasiopleura*) *conopsea* Duda. Apex of hind tibia and spur.

Figs. 17, 18.—*Lasiopleura* (*Lasiopleura*) *nudiseta* Becker. 17, Arista; 18, apex of hind tibia and spur.

Fig. 19.—*Lasiopleura* (*Lasiopleura*) *fuscipes* Malloch. Apex of hind tibia and spur.

Type and 1 paratype, Geraldton, W.A., 5.ix.1926 (E. W. Ferguson).

In the specimens of *ornatipennis* I have before me the fifth tergite also is silvery on the sides.

LASIOPLEURA (LASIOPLEURA) BRUNNEICOSTA Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, xlviii, 1923, 620.

I have seen no additional specimens that I can refer to this species. Described from Darwin, N. Territory, Australia.

LASIOPLEURA (LASIOPLEURA) ALBISETA Malloch. Fig. 11.

Op. cit., xlix, 1924, 330.

I have seen two additional specimens of this species from the type-locality, Eidsvold, Queensland. Apex of hind tibia and spur as Figure 11. It may have no significance, but appears to be worth noting here that both these specimens are mounted along with a specimen of *Drosophila albostriata* Malloch.

LASIOPLEURA (LASIOPLEURA) RUFESCENS Duda. Fig. 12.

Arb. Morph. Taxon. Ent. Berl.-Dahl., i, 1934, 49.

I have nothing to add to what I said regarding this species in Part xxxv of this series of papers. Type-locality, Darwin, N. Territory, Australia. Arista as Figure 12.

LASIOPLEURA (LASIOPLEURA) GRISEOVITTA Malloch. Fig. 13.

PROC. LINN. SOC. NEW SOUTH WALES, lxi, 1936, 25.

I had only the male before me when I described this species. I have put it in my key in three captions to take care of possible interpretations of its characters in both sexes. The hairs on the aristae are longer than is the rule in the *nudiseta* group, but they are not as dense on the basal half as in *nigripila* and *duplicata*, nor are they twice as long as the basal diameter of the aristae, though they are distinctly longer than in *nudiseta*. The female before me has the mesonotum with two narrow grey-dusted vittae along the dorsocentral lines and the remainder of the surface brownish-red. In other respects it agrees very closely with the male though the antennae and palpi are not so pale yellow. Apex of hind tibia and spur as Figure 13.

Locality the same as the type-specimen, Mt. Molloy, Queensland (F. H. Taylor).

There is some sexual dimorphism in one or two other species of the genus.

LASIOPLEURA (LASIOPLEURA) NIGRIPILA Duda.

Arb. Morph. Taxon. Ent. Berl.-Dahl., i, 1934, 48.

I have nothing to add to my note on this species in Part xxxv of this series of papers. Type-locality, Darwin, N. Territory, Australia.

LASIOPLEURA (LASIOPLEURA) DUPLICATA Malloch. Fig. 14.

PROC. LINN. SOC. NEW SOUTH WALES, xlviii, 1923, 621.

Known from only the type-specimen. Melville Is., N. Territory, Australia. Arista as Figure 14.

LASIOPLEURA (LASIOPLEURA) AEQUALIS Becker. Fig. 15.

Ann. Mus. Nat. Hung., ix, 1911, 111.

Originally described from Sydney from which locality I have already recorded it. I have seen additional material from Como, N.S.W., Blundell's, Molonglo R. and Canberra, Australian Capital Territory. Arista as Figure 14, apex of hind tibia and spur as Figure 15.

LASIOPLEURA (LASIOPLEURA) CONOPSEA Duda. Fig. 16.

Arb. Morph. Taxon. Ent. Berl.-Dahl., i, 1934, 45.

I have nothing to add to my note on this species in Part xxxv of this series of papers. Type-locality, Darwin, N. Territory, Australia. Apex of hind tibia and spur as Figure 16.

LASIOPLEURA (LASIOPLEURA) SETICAUDA Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, liii, 1928, 302.

Originally described from Sydney, N.S.W., and Warburton, Victoria. I have six additional specimens from Sydney.

LASIOPLEURA (LASIOPLEURA) ANOMALA Malloch.

Op. cit., l, 1925, 96.

This quite exceptional species presents a difference in the wing-venation of the sexes that I find in no other species known to me. I had only females before me when I described it, so did not know of the distinction in the sexes.

In the male the marginal cell of the wing is considerably wider than in the female, the second wing-vein is more abruptly curved forward at its apex, and the third vein sweeps downward at its base causing the base of the first posterior cell to be much narrower than in the female.

Originally described from Blue Mts., N.S.W., and Mt. Eba, S. Australia, I have several male specimens from Mt. Eba, apparently belonging to the same collection as the original type lot from that locality.

LASIOPLEURA (LASIOPLEURA) TAYLORI, n. sp.

♂. Very similar in most respects to *parva*. General colour and structure the same, the frons reddish-yellow on anterior half or more, genae the same colour. Uppermost of the three pairs of orbitals much longer than usual; gena more than half as high as eye, with two equal vibrissae. Thorax shiny-black, with rather even brownish-grey dust, the mesonotum not vittate. Anterior acrostichals minute, biseriate, not decussate; presutural bristle long. Legs brownish-yellow, femora largely infuscated. Hind tibial spur quite strong, curved, nearly as long as tibial diameter. Wings brownish-hyaline, veins dark brown; apical section of fifth vein more than two-thirds as long as preapical. Halteres yellow. Abdomen glossy-black. Hypopygium globose. Length, 2 mm.

Type, Blue Mts., 13.iv.1922 (Health Dept.); paratype male, greasy, Hampton, N.S.W., August 1932 (F. H. Taylor).

LASIOPLEURA (LASIOPLEURA) PARVA Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, liii, 1928, 302.

A small species very similar to the one described above, but here the hind tibial spur is longer and stronger and there are one or two of the presutural acrostichal bristles long and strong. Originally described from Sydney, and no new material to hand.

LASIOPLEURA (LASIOPLEURA) PARVA, var. PALLIPES, n. var.

This variety differs from the typical form in having the legs entirely honey-yellow. The genae appear to be more narrowed in front also, but having only one specimen of each form available I do not care to go farther into details. Length, 2 mm.

Type, Narrabeen, Sydney, N.S.W., 21.vii.1923 (Health Dept.).

LASIOPLEURA (LASIOPLEURA) NUDISETA Becker. Figs. 17–18.

Ann. Mus. Nat. Hung., ix, 1911, 113.

I have two additional specimens of this species, Wahroonga, Sydney. Type-locality, Sydney. Arista as Figure 17, apex of hind tibia and spur as Figure 18.

LASIOPLEURA (LASIOPLEURA) FUSCIPES Malloch. Fig. 19.

PROC. LINN. SOC. NEW SOUTH WALES, xlix, 1924, 330.

Originally described from Sydney and Milson Is. I have seen some additional material from the first-mentioned locality. Apex of hind tibia and spur as Figure 19.

EPHYDROSCINIS Malloch.

Op. cit., xlix, 1924, 331.

I have seen no additional specimens of this genus, nor can I say whether *raymenti* Curran belongs to the genus, as I have not seen the species. If the latter belongs to *Lasiopleura* it will run down to either *ornatipennis* or *exquisita*, but should be distinguishable from either of them by the entirely black femora and tibiae and brown tarsi.

THYRIDULA Becker.

Ann. Mus. Nat. Hung., ix, 1911, 94.

This genus may be distinguished from others by the presence of four or more short warts at the apex of the scutellum which bear stiff bristles at their apices, the apical pair usually much longer than the others, and in the typical subgenus by the fact that the tarsal claws on the hind legs are much longer and stronger than those on the other legs, and much curved, sickle-like.

There are four described species of the genus, all of them being readily distinguished from the genotype by the yellow, instead of black, ground-colour of the thorax. The genotype was described from New Guinea.

Key to the Species.

1. Hind tarsal claws about as long and strong as the fore and mid pairs; scutellum parallel-sided on basal half or more, rounded at apex, with four small warts on apical edge, the hairs surmounting these quite short and subequal .... *T.* (*Euthyridula*) *rugosa* Malloch

   Scutellum narrowed gradually from base to near apex, the apex with two rather closely placed short warts on the apex of each of which there is a rather long bristle, the sides each with three to five much smaller warts on which there are setulae shorter than the apical pair; hind tarsal claws about twice as long and strong as the fore and mid pairs, much curved 2

2. Scutellum with a complete black central stripe; face black in centre; at least the mid and hind femora preponderantly black ... *T.* (*Thyridula*) *centralis* Malloch

   Scutellum blackened on apical half or less: femora yellow, or partly browned 3

3. Face and hind tarsi entirely yellow; frons yellow, the ocellar spot black .... *T.* (*Thyridula*) *atroapicata* Malloch

   Face blackened in centre; apical two segments of hind tarsus black, remainder yellow; frons dark dull brown, yellow on anterior margin, the ocellar spot black ..... *T.* (*Thyridula*) *brunneifrons* Malloch

THYRIDULA (EUTHYRIDULA) RUGOSA Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, li, 1926, 546; op. cit., lii, 1927, 441.

Known only from North Queensland.

THYRIDULA (THYRIDULA) CENTRALIS Malloch.

Op. cit., l, 1925, 96.

Originally described from Sydney. I have seen additional specimens from Yass, N.S.W., 27.iii.1930 (K. English), and Black Mt., A.C.T., 13.iv.1931 (A. L. Tonnoir).

THYRIDULA (THYRIDULA) ATROAPICATA Malloch.

Op. cit., xlix, 1924, 358.

Originally described from Bowral, N.S.W. I have specimens before me from Yass, N.S.W., 10.iii.1930, and 2.i.1930 (K. English); and a slightly teneral specimen mounted on the same card with a damaged Ichneumonid labelled Eidsvold, Queensland, 29.iv.1930 (T. L. Bancroft).

THYRIDULA (THYRIDULA) BRUNNEIFRONS Malloch.

Op. cit., lii, 1927, 442.

I have only the type-specimen of this, from Tasmania, before me.

DELTASTOMA Malloch.

Op. cit., xlix, 1924, 359.

The peculiar V-shaped mouth-opening of this genus distinguishes it from all the other Australian genera of this subfamily. Both species have the wings marked much as in *Caviceps punctipennis* Duda, and the venation is also similar. In both genera there is a short setule above the upper posterior notopleural bristle, and the eyes are densely short stiff-haired.

The two species may be separated as below.

A. Antennae entirely yellow; mesonotum yellow, not vittate ..... *unipuncta* Malloch
AA. Antennae yellow, third segment black; mesonotum with four fuscous vittae ..... *atricornis* Malloch

DELTASTOMA UNIPUNCTA Malloch.

Op. cit., xlix, 1924, 359.

The type-specimen was from Sydney, from which locality I have seen a second specimen.

DELTASTOMA ATRICORNIS Malloch.

Op. cit., lvi, 1931, 66.

I have seen only the type specimen, from Sydney.

CAVICEPS Malloch.

Op. cit., xlix, 1924, 355.

There are two species known to me. They may be separated as below.

A. Wings entirely hyaline ..... *flavipes* Malloch
AA. Wing with a small rounded deep-black spot on the costa between apices of second and third veins ..... *punctipennis* (Duda)

When I described the genus I stated that *Oscinella defecta* Becker from the East Indies probably belonged here. The species is unknown to me.

CAVICEPS FLAVIPES Malloch.

Op. cit., xlix, 1924, 356.

Type locality, Sydney. I have before me a second specimen from Sydney.

CAVICEPS PUNCTIPENNIS (Duda).

Arb. Morph. Taxon. Ent. Berl.-Dahl., i, 1934, 56.

Erroneously placed in *Aprometopis* Becker by Duda.

Type locality, Darwin (Palmerston), N. Territory, Australia. I have seen this species.

It may be noted here that in both species of *Caviceps* the bristles on the head and thorax are yellow, while in the two species of *Deltastoma* now before me these bristles are black. In both genera the eyes are densely short stiff-haired.

There is an upwardly-curved upper humeral bristle sometimes present in *Caviceps*, but the presence of but one pair of dorsocentrals and two posterior notopleurals will serve to distinguish it from *Lasiopleura*.

Madiza Fallen.

Sp. Ent. nov. Dipt., 1810, 19.

This is the genus generally listed under the name *Siphonella*. Although the genotype and certain other species referred here are readily distinguished from others in the same section of the family by the typically produced epistome, short face as compared with the occiput, and the long, geniculated, slender proboscis, there are some species that have been placed in the genus that are undoubtedly but distantly related to the genotype. Some such species have been placed herein merely on the basis of the elongate proboscis, which in itself is rather an unreliable character as it varies to a considerable extent in both length and thickness. However, there is one Australian species that is so closely related to the genotype and so similar to it in almost all particulars that I have no hesitation in placing it here. In fact it may yet be proven that it is identical with one of the already described species, but meanwhile I consider it better to describe it as new, pending discovery of more specimens and some data on the life-history.

Madiza australis, n. sp. Fig. 20.

♂. An entirely shiny black species, with the frons dull brownish-black, the ocellar triangle grey-dusted; antennae, palpi, proboscis, and legs black, the mid and hind tarsi slightly brownish; knobs of halteres blackened above; wings hyaline, veins except ultimate section of fifth brownish-black. Head in profile as Figure 20; face with a triangular wedge-shaped carina between the bases of antennae that extends to below middle, the lateral edges raised; frons a little more than one-third of the head-width and about 1·5 times as long as wide, parallel-sided, the hairs short and dense, triangle confined to upper third, shiny, with greyish dust, ocellar bristles very short, irregular, verticals short. Eyes densely pale-haired. Thorax and scutellum densely piliferous-punctate, the latter short, rather narrow at apex, with two quite closely placed apical and two very much shorter preapical bristles; mesonotum slightly, upper part of mesopleura more distinctly, grey-dusted. Legs normal; mid tibial apical ventral bristle short. Wings hyaline. First costal section three-fourths as long as second, and a little longer than third, the latter about 1·5 times as long as fourth. Fourth vein ending almost in the wing tip, third slightly before it; penultimate section of fourth vein a little longer than penultimate section of third, about twice as long as outer cross-vein and one-fourth as long as ultimate section; ultimate section of fifth vein very much weaker and two-thirds as long as preceding section. Abdomen broadly ovate, depressed, more distinctly shiny than the mesonotum, and with some very short pale fine hairs. Length 2 mm.

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

The genus is almost cosmopolitan in its distribution and the genotype, if correctly recorded, occurs in the Palaearctic and Nearctic regions. I can not distinguish European and North American specimens as distinct species.

Tricimba Lioy.

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

I have already presented a key to the species of this genus from Australia and have nothing to add to the data on it except that I have a single specimen of a species that may be distinct from any that I have previously identified from this continent.

Cadrema Walker.

Jour. Proc. Linn. Soc. London, iv, 1860, 117.

I have presented already a key to the species of this genus known to me, but have before me now two additional species which are described below and give an enlarged key to the Australian species. I follow recent custom in the use of *Cadrema* instead of *Hippelates*.

All the species have a distinct, though often quite small and inconspicuous, apical ventral spur on the hind tibia which should be carefully looked for as it is easy to overlook it even with a high-power lens. The species from Australian localities are not at all closely related to the common type in North America which is suspected of carrying disease of the eye; all the New World forms that annoy one by buzzing round the face during hot weather have the hind tibial spur much more pronounced, and in several other respects differ from those now under discussion.

Key to the Species.

1. Third antennal segment entirely deep-black; hind tibial spur brownish-yellow, not as long as the apical width of the rather thick tibia, quite stout and curved, situated close to apex; mesonotum with three glossy-black vittae on a yellow ground, the central one complete, the laterals abbreviated at each extremity and slightly interrupted at suture ..... *atricornis* Malloch

   Antennae either entirely yellow or with a very slight darkening of the upper edge of the third segment; hind tibial spur black 2

2. Hind tibial spur much curved and distinctly longer than the tibial diameter, situated well before the apex; thoracic dorsum with a large quadrate mark in centre of hind margin and a spot near each humeral angle deep black, the ground colour yellow ..... *bancrofti* Malloch

   Hind tibial spur not as long as the tibial diameter, slightly curved and situated at or very close to the apex; thorax not marked as above 3

3. Mesonotum with rather coarse piliferous punctures, the scutellum slightly rugose or uneven; mesonotum largely black, ground colour yellow; scutellum partly black 4

   Mesonotum and scutellum with a few weak setigerous punctures, sparsest on scutellum; disc of mesonotum with distinct black vittae on a yellow ground; scutellum yellow; sternopleura partly or entirely yellow 6

4. The black mesonotal vittae fused on their entire length, only the lateral margins yellow, the postsutural black vittae separated narrowly from the central black complex mark; scutellum broadly black across the base; sternopleura entirely glossy-black ..... *nigridorsata* Malloch

   Mesonotal black vittae separated on disc 5

5. Mesonotum with three or five black vittae; scutellum almost entirely black; sternopleura entirely glossy-black; abdomen black, with yellow fasciae ..... *fasciventris*, n. sp.

   Mesonotum with two broad black vittae separated on disc by a broad orange-yellow streak, partly fused behind; scutellum broadly yellow at apex; sternopleura yellow; dorsum of abdomen glossy-black ..... *atriventris*, n. sp.

6. Pleura entirely yellow, without black markings; mesonotum yellow, with a linear black anchor-like mark in centre that does not extend to hind margin; frontal triangle glossy-black ..... *atriseta* Malloch

   Pleura with at least one black mark; mesonotum not marked as above 7

7. Sternopleura largely black centrally, two black spots on mesopleura, and one on pteropleura; mesonotum yellow, with a large U-shaped black mark from anterior to near posterior extremity, the free ends behind, and two small black marks between the latter behind the suture ..... *abbreviata* Malloch

Sternopleura yellow, only one black pleural mark present 8

8. Tibial spur of moderate length; mesonotum yellow, with two central black vittae that are fused and widened in front of suture, and on each side behind suture a short black sublateral vitta that is widened behind ..... *unimaculata* Malloch

Tibial spur minute; mesonotum yellow, with two broad black vittae that are almost interrupted at the suture and fused on posterior third, the fused part narrowed to hind margin ..... *fergusoni* Malloch

CADREMA FERGUSONI Malloch.

PROC. LINN. SOC. NEW SOUTH WALES, lii, 1927, 438 (*Hippelates*).

I have seen five additional specimens of this species from the type locality, Sydney (Health Dept.).

CADREMA FASCIVENTRIS, n. sp.

♀. Head orange-yellow, triangle black except a yellow mark on each side of ocelli at vertex; occiput with a black mark on each side above; third antennal segment with a faint apical suffusion, most evident at insertion of arista, the latter dark brown and pubescent; palpi orange-yellow. Frons about as long as its width at vertex, narrowed to anterior margin where it is a little more than one-third of the head-width, surface hairs black and quite strong, orbital setulae distinct above; ocellars shorter than postverticals; triangle to or very slightly beyond middle of frons. Eyes haired, higher than long; genae not as high as width of third antennal segment, with a series of black hairs on lower margin, the vibrissae quite strong. Thorax shiny yellow, mesonotum with the black vittae not well defined in type, appearing as three presuturally and five postsuturally, scutellum almost entirely black, and the pleura black except on propleura, but possibly darker than usual because of the pinning. Mesonotum and scutellum distinctly piliferous-punctate, the dorsocentral depressions broad behind. Notopleurals 1 + 2, scutellum with two long apical and two much shorter preapical bristles and some discal hairs. All hairs and bristles black. Legs yellow, quite strong, hind tibial spur black, not as long as tibial diameter. Wings hyaline, rather narrow, veins brown. First costal section more than four-fifths as long as second, the latter about 1·5 times as long as third; penultimate section of third vein not more than half as long as that of fourth and about as long as outer cross-vein; veins 3 and 4 slightly divergent at tips. Halteres yellow. Abdomen ovate, yellow, with a broad black fascia across centre of each tergite. Length, 2 mm.

Type, Sydney, N.S.W., 7.ii.1924 (Health Dept.).

CADREMA ATRIVENTRIS, n. sp.

♀. Head orange-yellow, a black mark on each side of upper occiput and a black central streak on triangle, third antennal segment narrowly dark at apex above, arista slender, brown, pubescent; palpi brown. Frons more flattened than in the preceding species, the triangle extending to almost the anterior margin and longer than its vertical width, a series of erect hairs just outside its lateral edges. All hairs black, stronger than in *fasciventris*.

Thorax glossy orange-yellow, with two broad black vittae that are not clearly defined in type, but the short sublateral postsutural vittae appearing as distinct, apical third or more of scutellum yellow, pleura yellow, with the anterior spiracle and a broad irregular fascia on lower part of upper half and the postnotum black.

Mesonotum and scutellum more coarsely piliferous-punctate than in *fasciventris*, the hairs and bristles as in that species. Legs orange-yellow, as in *fasciventris*. Wings hyaline, veins brown. First costal section about two-thirds as long as second, the latter subequal to third, marginal and submarginal cells at apex of first vein about equally wide, veins 3 and 4 not noticeably divergent at tips. Halteres yellow. Abdomen ovate, tapered at tip, genital processes slender, glossy-black in colour. Length, 2 mm.

Type, Donnybrook, W.A., 29.viii.1926 (E. W. Ferguson).

LIPARA Meigen.

Syst. Beschr. Zweifl. Insekt., vi, 1830, 1.

I have before me a species that closely resembles the genotype of this genus in general features and have no hesitation in placing it herein.

It looks like a very large *Conioscinella*, but differs from the members of that genus in having the genae about one-third of the eye-height, the parafacials well exposed in profile (Fig. 21), the frons more than half the head-width in front, narrowed behind, with the triangle continued narrowly as a grey-dusted stripe to beyond the middle of frons; the inner vertical bristles undeveloped; the mesopleura coarsely and irregularly vertically furrowed and almost entirely pale tomentose; scutellum subtriangular, highly convex on disc, and impressed along each side from near base to apex.

LIPARA AUSTRALIS, n. sp. Figs. 21, 22.

♀. Head dull brownish-black, anterior margin of frons narrowly brownish-yellow, occiput and triangle grey-dusted, the latter carried as a narrow stripe to or beyond middle of frons; genae and parafacials grey-dusted but changeable when seen from various angles; frontal orbits narrowly grey-dusted along eyes; hairs yellowish-white, a few of the upper orbital setulae and all the bristles black. Frons at vertex half the head-width, widened to anterior margin; triangle about one-third of the vertical width, not sharply outlined, some of the hairs on the edges of the grey-dusted part; inner verticals lacking in type-specimen, outer pair rather short, equal to the postverticals, the ocellars erect and weaker. Antennae brownish-yellow, third segment largely infuscated apically, about as long as wide and broadly rounded at apex; aristae fuscous, tapered from base to near middle, and bare. Face bifoveolate, the central carina high and quite sharp, widened and flattened between bases of antennae; parafacial in profile about half as wide as third antennal segment; gena fully one-third as high as eye, short-haired on lower two-thirds or more, vibrissae undeveloped. Proboscis glossy-black, not stout, geniculated, the apical section about two-thirds as long as lower margin of head; palpi long, brownish-yellow. Eye about 1·5 times as high as long, quite densely pale-haired. Thorax black, shiny, with brownish-grey dust, mesonotum with 4 or 6 black vittae, the central pair narrowly separated, the submedian pair wide, partly interrupted at suture, the sublaterals postsutural, indistinct; surface quite densely and rather coarsely piliferous-punctate, the hairs decumbent and pale; no humeral, notopleurals 1 + 2, postalars 2, dorsocentrals indistinct, and a series of bristly hairs along the posterior edge close to the deep suture between the mesonotum and scutellum, the latter subtriangular, prominently convex on disc and with a broad shallow impression on each side of apical half or more, appearing pinched in on sides, the apex with about six short bristles on minute wart-like elevated bases situated near the lower edge. Pleura glossy-black in part, grey-dusted on mesopleura, pteropleura, hypopleura, lower part of the sternopleura, and the mesopleura

rather coarsely vertically rugose. Legs brownish-yellow, coxae, greater part of femora, and middle of tibiae brownish-black, most extensively so on hind legs. Mid tibia with black apical ventral spur. Wings greyish-hyaline, brownish-tinged basally and costally, veins thick and brown, venation as Figure 22. Abdomen shiny black, quite densely grey-dusted, bases of tergites 3 and 4 blackened, more widely so on sides and centrally, tergite 5 with a large black shiny mark on each side at base. Hairs whitish-yellow, short above, longer below. Genital lamellae rather long and slender, with stiff, erect, bristly, blunt-tipped, black hairs on entire length. Halteres yellow. Length, 5·5 mm.

Type, Black Mt., A.C.T., 24.iv.1936, on nest of *Iridomyrmex defecta* (A. J. Nicholson).

It appears worthy of note that except in *Conioscinella griseopleura* the frons is parallel-sided in all Australian species of that genus. This particular species appears to be almost intermediate between the two genera, but most of its characters align it with *Conioscinella* rather than with *Lipara*.

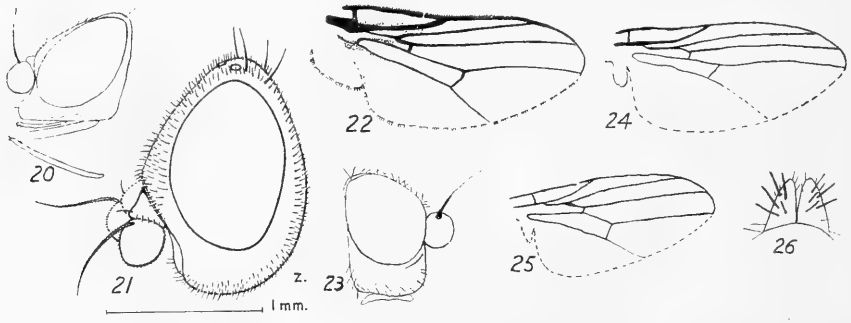


Fig. 20.—*Madiza australis*, n. sp. Head in profile.
Figs. 21, 22.—*Lipara australis*, n. sp. 21, Head in profile; 22, wing.
Figs. 23, 24.—*Conioscinella griseopleura*, n. sp. 23, Head in profile; 24, wing.
Fig. 25.—*Conioscinella pallidiseta*, n. sp. Wing.
Fig. 26.—*Conioscinella perdita*, n. sp. Genital processes of female.

Conioscinella Duda.

Folia Zool. Hydrobiol., ii, 1930, 71.

This genus, as I accept it on the basis of the characters of the genotype, contains a number of robust black species, with usually part of the legs and anterior edge of the frons brownish-yellow, the wings hyaline, frontal triangle small, usually dull, and not very sharply defined on the edges, frons haired, eyes distinctly pubescent, aristae pubescent to bare, the notopleural bristles 1 + 2, mesonotum sometimes closely piliferous-punctate, the hairs rather dense and indiscriminately arranged, not in well separated longitudinal series.

One of the species I place in the genus, *perdita*, is rather aberrant, the hairs on the disc of the scutellum being very few in number, and the convexity more marked than usual. Apart from this species there are two rather well marked segregates in the Australian material, using the wing venation as a criterion. In one, containing *pallidiseta*, *vandiemeni*, and *punctulata*, and possibly *griseopleura*, the fourth vein is noticeably deflected beyond the outer cross-vein so that for a variable distance the first posterior cell is wider there than it is about one-third from its apex, and the penultimate section of the third vein is not half as long as

the penultimate section of the fourth vein. In the other group the fourth vein is straight and gradually deflected to apex so that the first posterior cell is gradually widened to apex, and the penultimate section of the third vein is more than half as long as the penultimate section of the fourth.

Key to the Species.

1. Practically the entire mesopleura, all the pteropleura, and the sternopleura except behind, densely grey-dusted; ultimate and penultimate sections of fifth vein subequal in length; gena about one-fourth as high as eye, the vibrissal angle rounded; distance across the wing from apex of fifth to fourth vein about 1·5 times as great as distance from fourth vein to costa; scutellum convex, with many microscopic pale hairs ..... *griseopleura*, n. sp.
   Mesopleura in front and the entire sternopleura glossy-black; gena not one-fourth as high as eye, vibrissal angle generally produced 2
2. Legs entirely straw-yellow; all hairs and bristles on head and thorax luteous; ultimate section of fifth vein almost as long as penultimate; mesonotum shiny black, with even grey dust, the hairs not set in evident punctures .... *flaviseta*, n. sp.
   Legs not entirely yellow, in part black or dark brown; if the hairs and bristles of the head and thorax are luteous the mesonotum is without distinct grey dust and is very distinctly piliferous-punctate 2*a*

2*a*. Frontal and thoracic bristles and apical ventral spur of mid tibia fulvous-yellow; ultimate section of fifth vein about two-thirds as long as penultimate; gena about one-tenth as high as eye; scutellum flattened, densely and much more coarsely piliferous-punctate than the mesonotum, apical pair of bristles close together ..... *pallidiseta*, n. sp.
   Frontal and thoracic bristles black or dark brown 3

3. Entire frons dull black; genae not glossy below, entirely dull; outer cross-vein of the wing oblique, two-thirds as long as penultimate section of fourth vein; scutellum slightly flattened on disc, the apical pair of bristles separated by a distance greater than that across posterior ocelli, two shorter pairs on the sides and a number of fine discal hairs ..... *fuscofrontata*, n. sp.
   Frons yellow or orange-red in front; outer cross-vein about half as long as the penultimate section of fourth vein 4
4. Scutellum with two long and two slightly shorter preapical bristles, the disc with but two or four fine erect hairs; first section of the costa not more than half as long as second; genital processes spinose in female ..... *perdita*, n. sp.
   Scutellum with two long apical and two or more pairs of very much shorter laterals, the disc with many stiff decumbent hairs; first section of the costa much more than half as long as the second 5
5. Mesonotum with four uniformly broad black or black-brown vittae 6
   Mesonotum not distinctly vittate 7
6. Vittae shiny dark brown, intervening spaces lead-grey-dusted; halteres yellow; no dark cloud on apex of first wing vein ..... *mackerrasi*, n. sp.
   Vittae glossy-black, intervening spaces brownish-dusted; halteres brown; a faint brownish cloud on apical portion of first wing-vein ..... *emmesia*, n. sp.
7. Mesonotum closely and rather deeply piliferous-punctate; width of first posterior cell of the wing at the outer cross-vein equal to that of marginal and submarginal cells combined at same point 8
   Mesonotum almost smooth, not distinctly piliferous-punctate; first posterior cell of the wing at the outer cross-vein distinctly narrower than marginal and submarginal cells combined at the same point 9
8. Antennae, palpi, apices of the femora, fore and mid tibiae, and all the tarsi orange-yellow ..... *punctulata* Becker
   Antennae partly infuscated, palpi brown, all tibiae blackened centrally, and the tarsi brownish-yellow ..... *vandiemeni*, n. sp.
9. Mesonotum with the short hairs black or dark brown ..... *beckeri*, n. sp.
   Mesonotum with the short hairs whitish-yellow ..... *beckeri*, var. *grisella*, n. var.

CONIOSCINELLA PUNCTULATA (Becker).

Ann. Mus. Nat. Hung., ix, 1911, 158 (*Oscinella*).

I am accepting as this species a number of specimens that are of the usual robust form, and have the antennae, palpi, anterior margin of the frons and the greater part of the legs orange-yellow. The apices of the femora are usually quite broadly pale, and only the hind pair of the tibiae are browned centrally; the tarsi are entirely pale. The bristles of the head and thorax are black, the hairs on mesonotum short and stiff, mainly dark, those on posterior portion of humeri, and some on lateral margins, being yellowish-white and finer. The frons is about half the head-width in front, narrowed slightly behind; gena not as high as width of third antennal segment and about one-tenth as high as eye. Disc of mesonotum and scutellum distinctly and closely piliferous-punctate. Dust present on upper half or more of the mesopleura. Wings hyaline, veins fuscous. First costal section about two-thirds as long as second, penultimate section of fourth vein about three times as long as penultimate section of third, the inner cross-vein much proximad of level of apex of first vein; ultimate section of fifth vein about three-fourths as long as penultimate section. Length, 2·5 mm.

Five specimens, Sydney, N.S.W., January 1925 and November 1923 (Health Dept.).

CONIOSCINELLA GRISEOPLEURA, n. sp. Figs. 23, 24.

♂, ♀. Head black, frons not pale in front, narrowly grey-dusted along each eye, the triangle more densely dusted on edges than centrally, a grey-dusted line extending almost to anterior margin of frons; face grey-dusted; gena slightly brownish below, nowhere shiny, grey-dusted; frontal hairs white, bristles black. Triangle short, obcordate, not two-thirds as wide as vertex, and about one-third as long as frons, with stiff short black hairs invading surface almost to the ocelli; ocellars strong, a little shorter than the postverticals, the latter incurved; orbital setulae very short, pale to, or above, middle, from there to vertex black; surface hairs decumbent, directed mesially. Antennae black, third segment reddish-yellow below, wider than long, broadly rounded at apex. Arista with the basal two segments black, thick, second segment about four times as long as thick, third brown, slender and almost bare. Face rather deeply bifoveolate, carina in centre broad, flat above between antennal bases where it is about one-third as wide as anterior margin of frons. Gena about one-fourth as high as eye, with pale yellow hairs, vibrissae weak and short. Eye distinctly higher than long, rather densely pale-haired. Parafacial narrowly visible in profile (Fig. 23). Proboscis stout, glossy-black, geniculated; palpi black. Thorax black, slightly shiny, quite densely grey-dusted even on the sternopleura. Mesonotum with quite dense, rather small, piliferous punctures, the pile short, decumbent, and yellowish-white. Humeral bristle undeveloped, notopleurals 1 + 2. Scutellum short, round in apical outline, convex on disc, rather thin at apex, surface as that of mesonotum; apex with four short bristles. Legs black, knees, and tarsi except apices, tawny-yellow, black parts grey-dusted and with short pale hairs. Femora stout, mid tibial apical ventral spur strong, black, as long as apical diameter of the tibia. Wings greyish-hyaline, veins brown. Shape and venation as Figure 24, the exceptionally long ultimate section of fifth vein characteristic of the species. Abdomen stout, shiny black, with grey dust, and short pale hairs. Genital lamellae of female slender, slightly dilated at apices, of moderate length, with a few very fine hairs. Halteres with yellow knobs. Length, 3 mm.

Type, ♂, and allotype, Forrest, Canberra, A.C.T., 29.xii.1929 (A. L. Tonnoir).

CONIOSCINELLA PALLIDISETA, n. sp. Fig. 25.

♀. Head black, frons rather broadly orange-red in front, antennae except upper apical part of third segment, and the entire palpi, orange-red, genae broadly shiny brownish-red below, grey-dusted above; triangle slightly grey-dusted, face grey-dusted in foveae. Frons parallel-sided, a little more than one-third of the head-width and about 1·25 times as long as wide, triangle very small, extending about two-fifths of the frontal length and about half the width of vertex, no hairs invading its surface; bristles as in *griseopleura*, but the short setulae along the eye-margins are all black, the vertical and postvertical bristles are yellow, and the short frontal hairs are mainly black, posteriorly. Third antennal segment a little wider than long, rounded at apex; aristae black, tapered at base, with very short dense black pubescence. Face quite deeply bifoveolate, the central carina linear, not flat above, and much narrower there than in *griseopleura*; the epistome produced as in the genotype from Europe. Gena about one-tenth of the eye-height, with a series of short black hairs above lower edge and a short black vibrissa. Eye a little higher than long, with short stiff pale hairs. Proboscis glossy-black, stout, geniculated. Thorax black, shiny, mesonotum almost glossy, the dust most evident on the dorsocentral lines and lateral margins, only the posterior upper portion of mesopleura, the pteropleura and hypopleura grey-dusted. Mesonotum quite densely but not coarsely piliferous-punctate, the pile black in front and on disc, yellow behind, and laterally behind suture. Humeral, notopleural (1+2), postalar, and dorsocentral bristles yellow. Scutellum slightly elongate, narrowly rounded at apex, disc slightly flattened and much more densely and coarsely piliferous-punctate than the mesonotum, especially apically, the hairs black, the two long apical and two short preapical bristles yellow. Legs rather stout, coxae, femora except their extremities, and middle of hind tibiae, blackish-brown, remainder fulvous-yellow; hairs pale. Wings hyaline, veins brown. Venation as Figure 25. Abdomen glossy brownish-black, with short yellowish hairs. Genitalia of female as in *griseopleura*. Halteres yellow. Length, 2·25 mm.

Type, Eaglehawk Neck, Tasmania, 17.xi.1922 (A. L. Tonnoir).

CONIOSCINELLA FUSCOFRONTATA, n. sp.

♀. Head black, frons dull, not yellow in front, triangle hardly shiny, greyish-dusted, genae blackish-brown, paler above, nowhere shiny; antennae black, third segment reddish-yellow, infuscated above and at apex; aristae fuscous; hairs and bristles black. Frons parallel-sided, a little longer than wide, and more than one-third of the head-width; triangle less than half the frontal length, and about three-fifths the width of vertex, without surface hairs. Ocellar bristles rather strong, slightly reflexed, not as long as the postverticals, the latter a little longer than the outer verticals, the inner verticals very small; surface hairs on frons stiff, rather dense, the setulae along each eye-margin short, the uppermost about as long as the inner vertical. Antennae inserted a little below middle of eye in profile, third segment broader than long, broadly rounded at apex; arista with the second segment thicker than base of third, about four times as long as thick, third subnude, entire aristal length about four-fifths that of anterior width of frons. Eyes higher than long, with short stiff pale hairs. Parafacial not visible in profile. Face deeply bifoveolate, the central carina linear, widened above but not flat. Gena about one-seventh of the eye-height, angular in front, with two or three series of black hairs and a short black vibrissa. Thorax shiny black, lightly grey-dusted, under a high power lens appearing minutely alutaceous, with quite dense

fine decumbent black hairs not set in punctures, the hairs longer and denser posteriorly; notopleurals 1+2. Pleura shiny, mesopleura behind greyish-dusted, appearing alutaceous or microscopically striate. Scutellum shorter than its basal width, tapered behind, almost transverse between apical pair of bristles, the latter longer than scutellum, rather widely separated and cruciate, each side with one shorter bristle, and close in front of the latter a short setule, the disc flattened, like the surface of mesonotum but the hairs sparser and stronger. Legs brownish-black, fore tibiae brown, bases of tarsi brownish-yellow. Apical ventral spur of mid tibia about as long as apical diameter of tibia. Wings brownish-hyaline, veins brown. Second costal division about 1·5 times as long as first and nearly twice as long as third, the latter about one-fourth longer than fourth; penultimate sections of third and fourth veins subequal in length; outer cross-vein oblique and about three-fourths as long as penultimate section of fourth vein, ultimate section of fifth vein about two-thirds as long as penultimate. Abdomen shiny black-brown, the hairs dark. Genital lamellae slender, finely haired. Halteres with the knobs whitish-yellow. Length, 2 mm.

Type, Sydney, N.S.W., 25.ix.1921 (Health Dept.); paratype, S. Australia (A. H. Elston). The paratype appears to have been in liquid at some time, is badly abraded, and lacks the antennae.

CONIOSCINELLA MACKERRASI, n. sp.

♂, ♀. A very distinctively marked species, the four broad parallel-sided dark-brown shiny vittae on the mesonotum setting it apart from any other species in the genus, or in the genera related to it. The intervening spaces are lead-grey-dusted which is not the case in the next described species, and another feature that distinguishes it from the latter is the very much less shiny surface of the dark vittae which appear microscopically granulose here while in *emmesia* they are polished and smooth as if abraded. Frons dull brownish-black, reddish-yellow on anterior margin, with a grey-dusted lateral line on each side in front and in centre from ocelli to the pale anterior part; antennae brownish-black, third segment reddish-yellow basally below, more widely so in female; palpi brown in male, reddish-yellow in female. Frons a little longer than wide, about two-fifths as wide as head, with the usual stiff hairs, the vertical and ocellar bristles moderately strong, each orbit with about six stiff erect setulae. Eye higher than long, with numerous pale hairs. Gena brown, paler and whitish-grey-dusted above, not as high as width of third antennal segment, and about one-seventh as high as eye. Antennae moderately large, the aristae subnude. All hairs and bristles dark. Mesonotum rather flattened, the dark brown vittae almost entire, the laterals slightly abbreviated in front. All hairs and bristles dark. Surface hardly punctate. The usual bristles present, humeral moderate, both posterior notopleurals distinct. Legs black, in male with the tarsi slightly paler, brown, the bases and apices of the tibiae, and all the tarsi, fulvous-yellow in female. Wings hyaline, veins brownish-black. First costal section in male about two-thirds as long as second, in female about three-fourths, penultimate section of fourth vein a little longer than penultimate section of third, first posterior cell widened slightly to apex, ultimate section of fifth vein about two-thirds as long as penultimate one in male, comparatively shorter in female. Halteres yellow. Abdomen brownish-black, shiny, with apices of the tergites brownish. Length, 1·5–2 mm.

Type, male, allotype, and four paratypes, Sydney, N.S.W., the type and allotype taken in September 1924, the others on different dates in same year. Health Dept.

CONIOSCINELLA EMMESIA, n. sp.

♀. Very similar to *mackerrasi*, differing markedly in having the mesonotal vittae glossy and smooth as if abraded, the frontal triangle more distinctly shiny, the frons with a more distinct central pale line, which is broader and in some cases almost yellow and spot-like just in front of the triangle, the genae are paler, yellow, and the vibrissal angle more pronounced. The five specimens appear slightly teneral and have the legs dirty yellow, with no distinct black markings, but the brown knobs of the halteres suggest that the specimens are mature. Wings as in *mackerrasi*, but the ultimate section of the fifth vein a little longer in comparison with the penultimate one. Length, 2 mm.

Type and four paratypes, Sydney, N.S.W., August 1924 (Health Dept.).

One specimen has the second vein forked near its apex. It may be worth noting that with one exception, taken in May, all the specimens of *mackerrasi* were taken in September and October.

CONIOSCINELLA VANDIEMENI, n. sp.

♂, ♀. A shiny-black species, with the antennae black except the lower basal portion of the third segment, and the legs largely black, only the extremities of the tibiae, and the tarsi, pale brown. Halteres brownish-yellow. Frons distinctly longer than wide, parallel-sided, and about one-third of the head-width, narrowly brownish-yellow in front, with the usual stiff surface hairs, the palpi brown. Genae brown, paler above, not half as high as width of third antennal segment and about one-tenth as high as eye, the vibrissal angle slightly produced; eye much higher than long, finely soft-haired. Thorax shiny-black, the mesonotum densely piliferous-punctate, the hairs dark. The type female showing traces of four slightly more shiny stripes that in abraded specimens may show as vittae, the central pair abbreviated behind. Wings hyaline, veins black, the venation much as in *mackerrasi*, but the first posterior cell is widened beyond the outer cross-vein, and again slightly at apex. Length, 1·75 mm.

Type, female, Eaglehawk Neck, 15.xi.1922; allotype, Burnie, Tasmania, 25.x.1922 (A. Tonnoir).

CONIOSCINELLA BECKERI, n. sp.

♂, ♀. A small black species, with the mesonotum distinctly shiny and almost without punctures at bases of the fine erect black hairs. The frons has the anterior margin more or less distinctly reddish-yellow, and the antennae are usually largely orange-yellow, the third segment variably infuscated above and in front. The legs are variable in colour, but the fore coxae in the male and all the femora in both sexes are blackened, while the tibiae are usually all broadly blackened in the male sometimes only the hind pair are blackened in the female. The knobs of the halteres are pale yellow. Frons a little longer than wide, about two-fifths the head-width, with the usual stiff black surface hairs, the lateral marginal setulae very short, the vertical and ocellar bristles short but strong, the ocellars as usual slightly bent back and placed a little behind the level of the anterior ocellus. Eye higher than long, erect, with the hairs very short and white; gena not half as high as width of the third antennal segment and about one-tenth as high as eye. Antennae of moderate size, third segment disc-like; arista thickened on basal third or more, minutely pubescent. Mesonotum hardly dusted, the upper half of mesopleura and the pteropleura with dark-grey dust; mesonotal hairs and bristles dark. Some distinct piliferous punctures in the two lines of dorsocentral depressions and on the scutellum. Legs normal; mid tibia with the usual short black apical ventral

spur. Wings hyaline, veins black. Marginal cell wider than submarginal a little beyond apex of first vein, the two combined distinctly wider than first posterior cell at the level of outer cross-vein, the latter cell gradually widened to apex; ultimate section of fifth vein about half as long as penultimate one. Halteres with yellow knobs. Abdomen glossy brownish-black. Length, 1·5–2 mm.

Type, male, allotype, and a large series of both sexes, Sydney, various dates September to February (Health Dept.), paratypes, Como, N.S.W.; Mt. Wellington, Mt. Field, Strahan, and Cradle Valley, Tasmania, November to February (A. L. Tonnoir). One paratype from Blundell's, A.C.T., has the anterior margin of the frons more broadly orange-yellow than usual and the antennae almost entirely of that colour, while the legs are also preponderantly fulvous yellow.

Conioscinella beckeri, var. grisella, n. var.

Differs from the typical form in having the entire face and genae as well as the frons except upper third or less, the antennae, and the tibiae and tarsi except the central portion of the hind pair, fulvous-yellow. The hairs on the frons and mesonotum are also yellowish-white. In other respects similar to the typical form. The mesonotum is also more distinctly, evenly pale-grey-dusted. Length, 1·5 mm.

Type, Sydney, N.S.W., 15.x.1924 (Health Dept.).

Conioscinella perdita, n. sp. Fig. 26.

♀. Resembles in general colour the variety described above, having the head, including the genae, antennae, palpi, the frons except above, orange-yellow, the ocellar triangle short, poorly defined in front, slightly shiny, and grey-dusted. Frons distinctly longer than wide, parallel-sided, about two-fifths as wide as head, with the usual hairs and bristles, the hairs in front pale, behind and the bristles black. Gena higher in front than behind, the vibrissal angle distinctly produced and with a yellow setule, height of gena at middle equal to the width of third antennal segment; eye with fine yellow hairs, higher than long and about six times as high as gena. Thorax shiny-black, with quite even and distinct grey-dust on mesonotum and upper portion of pleura. No evident piliferous punctures on mesonotum or scutellum, the hairs on former fine and dark, the scutellum convex on disc, with two moderately long and rather widely separated apical and two shorter preapical bristles, and two or four fine discal hairs. Legs orange-yellow, femora and centre of hind tibiae infuscated. Wings hyaline, veins pale brown, yellowish at bases; the first section of the costa not half as long as second. Halteres yellow. Abdomen shiny blackish-brown, with grey dusting, the apices of the tergites brownish-yellow. The genital processes of the female are spinose (Fig. 26). Length, 1·5 mm.

Type and one paratype, Ooldea, S. Australia, 20.viii.1926, no collector's name on the written label. Many paratypes from Sydney (Health Dept.), one from Molonglo River, A.C.T.

I have seen no other species of the genus in which the characteristic spines or bristles are present on the genital lobes of the female, though they may occur and I have not noticed them in specimens examined. Usually the presence of such genital spines or bristles indicates that the species deposits its eggs in openings made by the female in plants or other substances.

Conioscinella flaviseta, n. sp.

♂, ♀. A small black species with shiny-black evenly yellow-grey-dusted mesonotum, the cephalic and thoracic hairs and bristles luteous, and the legs yellow.

Head brownish-black, dull, with grey dust, anterior margin of frons, antennae, face, genae, palpi, and proboscis, brownish-yellow to orange-yellow. Frons at vertex about one-half the head-width, narrowed to anterior margin and about as long as its vertical width, triangle dusted and not defined, outer verticals longer than inner and postvertical bristles, the ocellars small, orbital setulae minute. Eyes haired, fully eight times as high as gena; vibrissal angle slightly produced; proboscis geniculate. Arista pubescent. Thorax with no punctures at bases of the dorsal hairs, the latter numerous and depressed; bristling normal, humeral long; scutellum convex on disc, rounded in outline with no punctures at bases of the few erect discal hairs and with two long apical and two much shorter preapical bristles. Postnotum glossy-black. Legs yellow. Mid tibial spur short, both it and all the hairs yellow. Wings hyaline, veins brown. First costal division a little more than half as long as the second and slightly longer than third, the latter a little longer than fourth; the fourth vein ending a little behind wing-tip, the third well before it; penultimate section of fourth vein about twice as long as penultimate section of third; first posterior cell slightly widened at apex; ultimate section of fifth vein nearly as long as penultimate section and at least twice as long as penultimate section of fourth vein. Distance from apex of fifth vein to fourth vein subequal to that from fourth vein to costa. Halteres yellow. Abdomen shiny black-brown, broadly ovate, with most of the hairs yellowish. The genital lamellae of female quite long and very slender, much as in *Lioscinella similis*, with some microscopic fine pale hairs and no bristles. Length, 1–1·5 mm.

Type, female, allotype, and 7 paratypes, Sydney, N.S.W., October-January (Health Dept.).

A rather aberrant species in this group, rather similar to *perdita* in some respects.

Oscinella Becker.

Archiv. Zool. Hungar., i, 1910, 150.

This generic name was proposed as a substitute for *Oscinis* of authors, not Latreille, and originally the concept included several subsequently recognized or acknowledged genera. Now it is restricted to much narrower scope, and in Australia there is apparently but one species known, the genotype, *frit* Linné. This species has several characters that distinguish it from its closest relatives, consisting of a glossy elongate frontal triangle, very short pubescent aristae, short-haired eyes, granular or alutaceous mesonotum with rather widely separated serially arranged fine hairs, a rather distinct bristly hair that is forwardly directed at the upper posterior angle of the sternopleura, and a general black colour.

Some, but not all of these characters are found in other genera, the most distinctive being the granular surface and serially arranged sparse hairs of the mesonotum. The sternopleural armature is the same in the group in which the scutellum is yellow or partly yellow and the triangle glossy and almost invariably black, and there is no forwardly-directed sternopleural bristle in *Conioscinella* and *Botanobia*.

Oscinella frit (Linné).

Syst. Nat., ed. 10, 1758, 598; ed. 12, 1767, 994 (*Musca*).

I can detect no differences between European, North American and Australian specimens of this species.

I have seen only two species correctly referable here, *frit*, in which the arista is entirely black or black-brown, and the third segment very short dark pubescent,

and *maura* Fallén, in which the basal two segments are black and the third white and quite long white pubescent. There are no records of *maura* from outside of Europe as far as I know.

In *frit* the whole insect is black except the apices, and sometimes the bases, of the tibiae, and the bases of the tarsi, which are yellow in varying degrees of intensity. Length, 1·5–2·5 mm.

Botany Bay, N.S.W.; Blundell's, A.C.T.

The larvae feed in the stems of cultivated grains such as wheat and oats.

ON THE EXTERNAL MORPHOLOGY AND BIOLOGY OF *HETERONYCHUS SANCTAE-HELENAE* BLANCH. AND *METANASTES VULGIVAGUS* OLLIFF (COL., SCARABAEIDAE, DYNASTINAE).

By D. Margaret Cumpston, M.Sc., Linnean Macleay Fellow of the Society in Zoology.

(Plate ix; twelve Text-figures.)

[Read 26th June, 1940.]

In the family Scarabaeidae of the Coleoptera, morphological work on the immature stages lags far behind taxonomic studies of the adults. By the "immature stages" is implied, in particular, the larval stages. Until fairly recently all Scarab larvae have been classed together in one group as "white curl-grubs" without serious attempt at specific differentiation. It is hardly necessary to point out that, in a group such as this where by far the greater part of the damage is caused by the larva, knowledge sufficient to permit immediate recognition of the larvae is invaluable. Adult damage is as a rule confined to the foliage of native trees, but that caused by the larvae includes a wide range of diverse plants. Illustrated morphological descriptions of various species of Queensland cane-beetle larvae have been published in some of the Bulletins of the Division of Entomology of the Queensland Bureau of Sugar Experiment Stations, but apart from these little work has been done in this direction in Australia.

Although work from the biological aspect has already been carried out on *Heteronychus sanctae-helenae* and *Metanastes vulgivagus* (for literature, see section dealing with life-history), knowledge of the external morphology of the immature stages is slight. In 1930 Burns published a short general description of the fully-fed third instar larva and of the pupa of *Metanastes vulgivagus*. In all stages the two species are similar in appearance as well as habits, which renders them easily confused. Such confusion has existed, and it was only recently that their identity in New South Wales as two separate species was established (Gurney, 1934). In the present paper are included descriptions of all stages of these species, with emphasis on the two destructive stages, the larval and the adult. It was considered advantageous to include a discussion of their bionomics, and also of the synonymy of *Metanastes vulgivagus*. These species are of particular interest, not only because of their comparatively short life-history, but because the adult is as a rule responsible for a greater amount of damage than the larvae.

Synonymy of Metanastes vulgivagus Olliff.

There has been in the past some confusion about the correct naming of this species. It was described by Blackburn in 1886 from South Australia under the name of *Pentodon australis*; in all the early literature and as recently as 1933 (McDougall, 1933) it is referred to as *Pentodon australis*. Olliff in 1889 recorded the same species from Lord Howe Island under the name of *Heteronychus vulgivagus*. In 1911 Arrow set up a new genus *Metanastes*, including two species,

Heteronychus australis Fauv., the type species from New Caledonia, and *Pentodon australis*. He suggested that the later described Australian insect (*Pentodon australis*) should be renamed *Metanastes blackburni*. It is the last name which appears in Gurney's paper of 1934, in which he discusses the synonymy of this species. Arrow later apparently decided that Olliff's original specific name should stand, as in the section on Dynastinae in the Catalogus Coleopterorum published in 1937, he uses the name *Metanastes vulgivagus* Olliff. The synonyms for this species are therefore *Pentodon australis* Blackburn, *Heteronychus vulgivagus* Olliff and *Metanastes blackburni* Arrow.

Economic History and Distribution.

Heteronychus sanctae-helenae Blanch. (*H. arator* Burm.—the black beetle) is an introduced pest species from South Africa, where it attacks maize and sugar-cane. Since 1930 it has spread rapidly in New South Wales and now occurs from the northern rivers south to Wollongong, in both coastal and inland districts. It was noted as a pest species in 1934 (Gurney, 1934), but had been causing appreciable damage four years prior to this. It has not been recorded in any State other than New South Wales as yet. This species is a major pest, attacking any lawn surfaces such as golf and bowling greens, also maize and sugar-cane, and vegetable crops such as cauliflowers and tomatoes; in addition it has been noted as attacking banana plantings and rose cuttings.

Metanastes vulgivagus Olliff (the black beetle, black set beetle, black stem gouger) is a native species first described from South Australia, where it is widely distributed, and also occurring in Lord Howe Island, New South Wales and Queensland. It ranks as a pest in the two latter States only. In New South Wales it was recorded as early as 1903 (Gurney, 1934), attacking maize seedlings at Richmond, and later as damaging sugar-cane in the Clarence River district, although the infestations were not heavy. There are few records of damage caused by *Metanastes vulgivagus* in New South Wales. In Queensland it attacks both maize and sugar-cane (recorded in 1912—Girault and Dodd, 1915), occurring as a minor and sporadic pest in practically all the sugar-growing districts of the State, but has not been recorded as a pest of other crops; at the present time it is not considered of considerable economic importance, although fairly extensive outbreaks have been reported (Gibson 1924, Mungomery 1927, 1929, Burns 1930).

Damage.

For these species it is invariably stated that the major part of the damage is caused by the adults, which attack in numbers the growing plants during the spring and early summer, boring into the stalk at any point beneath the surface of the ground. This results in a large ragged hole which, when the plant is young, will cause death; when the plant is older the boring action of the beetle, although it may not destroy a fatal amount of vascular tissue, will seriously weaken the plant.

Damage by the larvae of *Metanastes vulgivagus* has been reported. Burns (1930) states that in some instances as many as 4 and 5 final instar larvae of *M. vulgivagus* were found inside cane-sets; some had entered through the ends, while others had bored through the rind into the interior of the sets. Their tunnels may be several inches in length. The year previous to this, Mungomery stated that the larvae "ingest large quantities of soil and rotting vegetation before becoming full-grown, and it is from this rotting organic matter that they derive most of their nourishment. In addition to the beetles, these grubs are sometimes

responsible for injury to cane, and their chief damage consists of eating into the ends of cane sets and hollowing them out. Thus it will be seen that they are not essentially root-eaters". Jarvis (1927) stated that these larvae destroy the roots of cane sets, and gnaw big holes in the plants.

In no case has it been believed that damage was caused by larvae of *Heteronychus sanctae-helenae*. The question has been raised whether larvae of this species ever do attack the plant under field conditions, the usual assumption being that they can subsist upon decaying vegetable matter in the soil. This view is supported by the fact that all Scarab larvae ingest large quantities of soil, and probably do derive some nourishment from it. The writer, however, in March of the present year, observed a large area of turf (bent and couch grasses) in which the roots had been so completely destroyed that the turf could be pulled away in sheets from the ground. Immediately below was a heavy infestation of mature larvae of *Heteronychus sanctae-helenae*, together with pupae and recently emerged adults, some of which were not even completely darkened. There is no doubt that this damage was due to the larvae.

Under conditions in the insectary, larvae of both species (reared on maize) have been found to attack the grain both before and after germination, and the young shoots as well as the roots. Such extensive damage always results in the death of the plant. Preliminary experiments with *H. sanctae-helenae* and *M. vulgivagus* indicate that first and second instar larvae can exist upon what is derived from the soil alone. Experiments with *Euetheola rugiceps* Lec., a closely related North American species (Phillips and Fox, 1924), indicated that the normal food of the larvae consists chiefly of decayed and disintegrated vegetable matter, but this vegetable mould is consumed in inordinate amounts by the third instar larvae. It seems likely therefore that even if the normal food for all instars is decaying vegetable matter, where the supply of this in the soil is poor there will be insufficient for the voraciously-feeding third-instar larvae, and they will secondarily attack the living plants of their habitat.

In this connection the following facts are of interest. Fox and Ludwig (1937) stated that it had been possible to rear larvae of the Japanese beetle (*Popillia japonica*) from egg to adult on decayed vegetable matter alone, although in such instances development is somewhat retarded compared with that of larvae also supplied with other food, such as grains of wheat. In 1938 Fox and Ludwig published the results of a series of experiments with *Popillia japonica* larvae, in which they found that the suitability of the rearing medium used (decayed plant matter) appeared to be correlated with the taxonomic relationship to the grasses (Family Gramineae) of the plant furnishing this material. They further concluded that, since the addition of wheat or of yeast to a medium made it better for larval growth, these effects might possibly be due to the presence of accessory food factors belonging to the vitamin B complex.

Material and Methods.

The experimental and morphological work was carried out at the Zoology Department, University of Sydney, the field observations and collection of *Heteronychus sanctae-helenae* mainly at Moore Park, Sydney. Adults were also obtained from other Sydney localities, and from Broadwater, New South Wales. As a rule, they were hand-collected crawling on the ground surface between 7 and 9 a.m., in the months September to December. All adults of *Metanastes vulgivagus* used were collected at Harwood, and obtained through the kindness of the Colonial Sugar Refining Co., as were also those specimens of *Heteronychus*

sanctae-helenae from Broadwater. Larvae, pupae and newly emerged adults of the latter were collected from the Royal Sydney Golf Club links in March. Like all Dynastids, these species breed well in captivity and because of their comparatively short life-cycle should be good subjects for experimentation on food preferences, etc.

The subsequent discussion refers to both species. The adults were kept in flower-pots filled with finely-sifted soil, and covered with cylindrical wire-gauze cages. The beetles fed readily on maize, either on the grain before germination, or on the young shoots. Copulation and oviposition took place normally. The soil was kept moderately moist; when examined for eggs it was passed through a fine sieve, and because of their white colour the eggs were readily detected. This frequent disturbance may have some effect on the total egg yield, but did not affect their deposition.

The eggs were transferred by means of a moist camel's hair brush to small pits in soil, impressed most satisfactorily by the blunt end of a pencil. The soil is packed firm, the hatching box being about two-thirds full. The containers used were tobacco tins, the lid conserving the moisture in the soil. Water may be added by means of a dropper. Excessive moisture is unfavourable, encouraging fungal growth. Hatching can be anticipated by the appearance of mandibles and spiracles through the egg membranes. When hatching took place the larvae were removed to flower-pots containing finely-sifted soil. They were buried in the soil, because, although capable of burrowing, they survive better if actually buried. The number of larvae to a 6-inch flower-pot should not be more than ten. Larval mortality in the stocks is invariably high and, in addition, if they are overcrowded they will attack each other. When the larvae were well into the second instar, they were transferred again to small cylindrical tins 2″ by 3″, one larva to each tin. To obtain the periods between moults, larvae were isolated from the time of hatching, in similar tins. The larvae are resistant to handling, but overwatering must be guarded against. It is much easier to overwater than underwater, and superfluous moisture will kill the larvae. The actual amount of water necessary is a matter of experience and varies according to external conditions. Some larvae were reared to the third instar in soil in which there were no growing plants, but subsequent to that they were provided with maize. When the prepupal stage was reached all plants were removed from the soil.

Life-History and Habits.

Because of marked similarity of life-history and habits the two species will be considered together. There is only one main generation every year. Both species overwinter in the soil as adults. The precise time of emergence is variable, this being governed by prevailing weather conditions. In 1939 adults of *Heteronychus sanctae-helenae* were collected in the middle of September. Mungomery (1929) records deposition of the first egg batches of *Metanastes vulgivagus* towards the end of August. At this time the adults may cause considerable damage. They have been observed on the wing swarming at lights during the evening; they are usually to be found crawling on the surface of the ground in the early morning after sunrise, disappearing as the sun's rays become hotter. This activity explains repeated infestation of crops from adjoining paspalum land; normally migration does not take place on the wing. They burrow either into the ground again, or beneath heaps of dead leaves or tufts of grass. These burrowing habits in *Heteronychus sanctae-helenae* are responsible for much uneven pitting

on smooth lawn surfaces such as golf or bowling greens and tennis courts (similar damage has not been reported for *Metanastes vulgivagus*). The preferred habitat of both species is low-lying paspalum pasture, and damage to crops is heaviest when plantings are made on recently turned paspalum land which is already infested (*Agric. Gaz. N.S.W.*, 1934–1939, *Qd. Agric. J.*, 1924–1930). Any subsequent lessening of infestation which may occur is probably explained by the fact that intensive cultivation, in addition to destroying any immature stages then present, eventually renders soil conditions unsuitable for the larvae.

Copulation occurs beneath the surface of the ground, and may take place some weeks before egg deposition by the female. Almost the entire life-cycle is spent in the ground: the adults feed, mate and oviposit, and the eggs, larvae and pupae develop below ground level. Copulation occurs throughout the egg-laying season: pairs in coitu were recovered as late as the middle of December, from individuals kept in the insectary. Egg deposition extends over a considerable period of time, under these conditions almost certainly longer than in the field. During the current season, 1939–40, females laid continuously, a few eggs at a time, from October till the end of February. Eggs of *Metanastes vulgivagus* in particular were found during the latter part of this period. Swarming frequently takes place again in March; the young adults will sometimes feed prior to hibernation in the soil, but egg deposition does not take place at this time. The total developmental period for both species is approximately the same, and remarkably short when compared with other Scarabaeidae, which require at least 12 months for their life-cycle. In *Metanastes vulgivagus* and *Heteronychus sanctae-helenae* the period from egg deposition to adult is 3 or 4 months. It is interesting to note that an American maize and sugar-cane pest, *Euetheola rugiceps* Lec. (subfamily Dynastinae) has a very similar life-history and habits, overwintering in the adult stage and requiring the same developmental period (Phillips and Fox, 1924).

The incubation period for the eggs is three weeks early in the season (October–November), decreasing to two weeks in December. The incubation period when the eggs are kept at a constant temperature of 80°F. is 10 days. The eggs are laid either freely in the ground, probably as the female is feeding, or enclosed loosely in a pellet of earth. The eggs of *Metanastes vulgivagus* are more often enclosed than free. The eggs are always laid singly a few inches below ground level, never in batches in a chamber in the soil, as with other species. The largest number of eggs deposited by a single female of *Heteronychus sanctae-helenae* under insectary conditions was 90, laid irregularly over a period of four months, from November till the end of February. The male died at the end of November, yet the female continued to produce fertile eggs.

The larvae start feeding soon after hatching. They ingest quantities of soil, so that the gut soon takes on the characteristic dark colour. They are active and capable of burrowing almost immediately. There are three larval instars. The first instar occupies a period of approximately three weeks, the second two weeks, and the third (including the prepupal period) about six weeks. When the final instar larva is fully grown it enters the quiescent prepupal stage, first forming a pupal cell in the soil, and discharging the contents of the rectum; during this period it is capable only of abdominal flexion, and is of a uniform pale colour. The pupa develops inside this larval skin, and in some cases development is completed within it, a dorsal split appearing when the pupa is fully formed. Generally the larval skin is shed completely. The pupal period lasts approximately a fortnight.

Adults of the new generation are a highly burnished black, those of the old generation are dull and readily distinguishable from the former. Most of the latter die before the end of the season, but Mungomery (1929) recorded adults of *Metanastes vulgivagus* producing, under laboratory conditions, eggs over two seasons at least.

Morphology.

a. Adult.

The two species are superficially very similar. They are both typical Dynastids, glossy-black dorsally and reddish-brown ventrally, but are easily distinguished by structural differences. *Metanastes vulgivagus* is slightly though distinctly larger; the length of this species is 14–16 mm. *Heteronychus sanctae-helenae* is 11–13 mm. in length, the males being slightly smaller than the females. The general shape of the two species is also rather different, the former being more broad and flattened than the latter. The obvious structural difference between the two species is the presence of two cephalic tubercles in the former species, and their absence in the latter. A second difference lies in the puncturation of the elytra. In *Metanastes vulgivagus* there are 7 impressed rows of punctures, without counting the most extreme median row in which the puncturations are so deep that they form a striation. In *Heteronychus sanctae-helenae* there are 6 impressed rows. The presence or absence of the cephalic tubercles is the most reliable character, since the lengths are naturally very variable, and the elytral puncturation is also variable to a certain extent.

A striking feature common to both species is their sexual dimorphism. The male and female may be immediately differentiated by the shape of the fore tarsus. In the male the segments are shortened and flattened: one of the tarsal claws is simple, and the other is a broad bent lamina (Fig. 1). The tarsus of the female retains its normal filiform shape (Fig. 2): the deformity in the male is due to the use of the tarsi in copulation, the hooked tarsal claws being inserted beneath the elytra of the female. A less obvious sexual difference lies in the form of the pygidium, which in the male is broadly rounded and in the female is apically pointed.

b. Egg.

The eggs when freshly laid are elongate oval, almost oblong in shape. Swelling of the egg takes place almost immediately, doubtless due to absorption of water by the egg from the surrounding soil. At the end of three days there is quite marked swelling and the eggs have become almost spherical. There is a simultaneous increase along the major and minor axes; the total increase is greater along the minor axis. Several days prior to hatching the mandibles and spiracles of the young larva are visible through the chorion. For *Heteronychus sanctae-helenae* the chorion of the newly-laid egg is greyish-white in colour, sticky, shiny, and rather soft, with no markings except a faint pitting. The average size is 1·8 mm. in length and 1·3 mm. in width. Just before hatching the average length is 2·3 mm. and the average width 2·0 mm. The egg of *Metanastes vulgivagus* is appreciably larger, dead white in colour, and the chorion is tougher, but also without markings. The average size after laying is 2·3 mm. in length and 1·6 mm. in width. The average length before hatching is 2·8 mm. and the average width 2·4 mm.

c. Larva.

In general appearance the larva is typically scarabaeiform, creamy-white in colour except for the last two segments, which are black, due to the rectal contents showing through the thin integument. The general appearance of these larvae is too well known to need further comment. The hypognathous head is heavily chitinized with a well-differentiated epicranium and frons (Figs. 3, 4). The epistomal and clypeolabral sutures are quite heavily marked. The mandibles are reddish-brown, shading to black at the tips. The clypeus and labrum are slightly darker in colour than the rest of the head; the labrum is slightly asymmetric and not lobed. The chaetotaxy of the head is sparse. An oval stridulating area of transverse striae on the caudal side of the mandible (Fig. 5), and truncated stridulating teeth (the plectrum) on the cephalic side of the maxilla (Fig. 6) are present; these characters are postulated by Hayes (1929) as characteristic of the subfamily Dynastinae (see p. 44 of his monograph for discussion of the organs of stridulation). The larvae are supposed to emit sound by scraping one across the other. Dorsally each of the first six abdominal segments is divided into three subsegments, carrying short, stout, straight bristles together with a few scattered longer and more slender bristles. This dorsal chaetotaxy is only slightly variable and therefore has no systematic significance. The two regions of the body bearing important structural features are the head and the anal segment, the former including the epipharynx (Figs. 7 and 8; Plate ix, figs. 3, 4), and the latter the radula (Figs. 9 and 10), both of which have been found to be so variable that, taken in conjunction, they are valuable as a basis for the separation of genera and species, as has been shown by Hayes with North American species of Scarabaeidae.* His work was the first to demonstrate clearly the interesting and marked variations occurring in these two structures. The structure of the head capsule itself is also of diagnostic importance in some genera and species (Madle, 1935).

The radula is a specialized region situated ventrally on the anal segment of the body (Figs. 9 and 10), the function of which appears to be the cleaning of the mouth-parts. It occurs as arrangements of articulated bristles, which are very variable interspecifically. The radula is always considered in conjunction with the anal slit, which may be longitudinal, or transverse, that is, perpendicular to the longitudinal axis of the body. In both *Heteronychus sanctae-helenae* and *Metanastes vulgivagus* (Figs. 9 and 10) the anal slit is transverse, and immediately ventral to it is a clearly marked subanal flap, without a median series of differentiated bristles, agreeing with the characters for the subfamily Dynastinae set down by Subklew (1937). All bristles are articulated. The figures given for bristle numbers (see below) cover the most usual range found in these two species.

The epipharynx is a specialized sensory region, the membraneous inner wall of the labrum; in the descriptions of *Heteronychus sanctae-helenae* and *Metanastes vulgivagus* is also included a sensory area located on the inner wall of the clypeus (Figs. 7 and 8). This proximal sensory area is placed at the entrance to the pharynx and from its specialization is probably of considerable importance in perception of the nature of food ingested. It contains a rounded median tubercle, the sense cone, in which are visible four sensilla. On the right side of the sense cone (left in drawings) is present a pointed chitinous plate.

* The descriptive terms used are those of Hayes; see monograph of 1929 for account of epipharyngeal and radular variations in numerous species.

There are also present four clypeal sensilla and two groups of non-articulated clypeal hairs. The epipharynx is outlined proximally by the asymmetric tormae, which are heavily chitinized bars at the lateral extremes of the clypeolabral suture, the right long and narrow, tapering to a point just distal of the chitinous plate, the left very slightly curved and ending bluntly. There are also present lateral and median articulated setae, the latter surrounding a median bare space. The lateral setae are curved and fairly long, without striae at their bases (such as occur in larval Melolonthinae); and increase in size towards the distal series of relatively long and straight bristles. The number of bristles present in the epipharynx of either species is unimportant. The two species agree in all the points just outlined; the feature distinguishing *Metanastes vulgivagus* from *Heteronychus sanctae-helenae* is the shape of the distal sensory area (see below). The distal sensory area is located above the median bare space, and (within the family Scarabaeidae) may include various spines or bristles and sensilla, and is evidently a localized perceptive region. Epipharyngeal studies were carried out on specimens both before and after clearing. The drawings (Figs. 7, 8) and photographs (Plate ix, figs. 3, 4) were taken from Canada balsam mounts.

Comparative Morphology of the Larva.

Distinguishing features of Heteronychus sanctae-helenae *and* Metanastes vulgivagus.

These descriptions of epipharynx and radula are based on final instar larvae, since there is little difference in regard to these structures between the instars and within each species other than an increase in size, and a fairly marked increase both in thickness and number of bristles from first to third instar. Both structures are therefore described in the fully-developed condition. In the first two instars, although not completely developed, these diagnostic features are still quite sufficiently distinctive. The colour of the head capsule (and its puncturation in *Metanastes vulgivagus*) does not change, and was actually found an adequate character for separation of the two species in experimental work.

1. *Heteronychus sanctae-helenae.*

The average width of the head capsule of a first-instar larva (measured at the antennal bases) is 1·5 mm.; of a second instar larva is 2·4 mm.; the length of a fully-fed final instar larva is about 25 mm. (when extended as in the crawling position), and the average width of the head capsule 4 mm.

The head is light-brown in colour, and very finely reticulated, appearing smooth to the naked eye (Plate ix, fig. 2). It has a few scattered punctures on the frons, clypeus and labrum. On the frons are 14–20 short and long bristles (Fig. 4), not including the 2–3 bristles situated on each side of the head between the antennal bases and the articulation of the mandibles. The disposition of these frontal bristles varies.

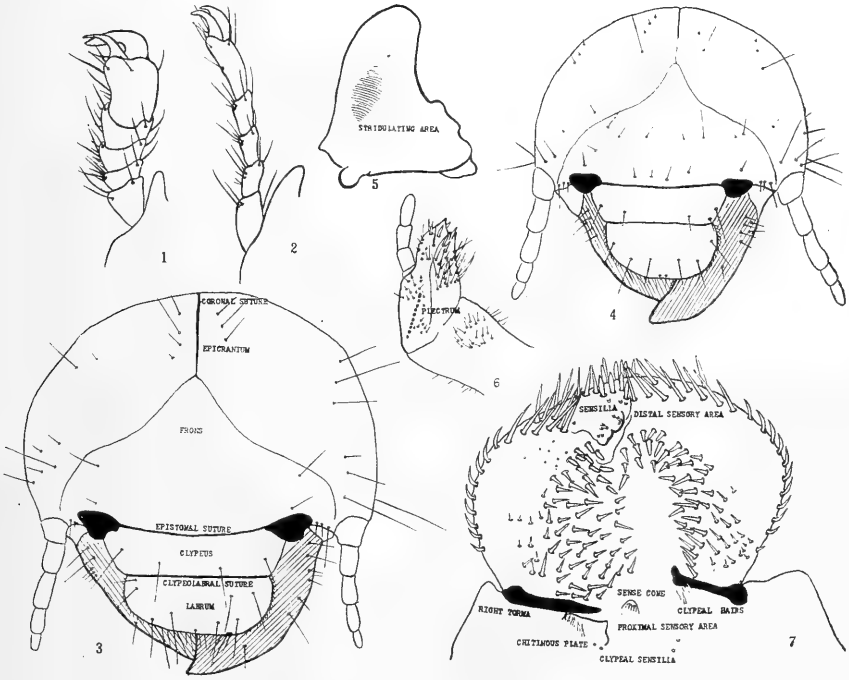
The distal sensory area is a humped chitinous area ending in a single large projection directed proximally, without teeth or spines, but bearing on the right (left in drawings) a group of closely set stout bristles. This projection is usually bifid, and may be trifid. The bristles at the apex of the epipharynx are short and thick (Fig. 7).

The subanal flap carries, on the lower lip of the anus, a row of about 12 long fine bristles (Fig. 9); the rest of the area is occupied by 35–40 shorter and stouter bristles. Dorsal to the anus is a longitudinal bare space, and on either side of this a patch of 20–25 short straight bristles and, laterally, groups of

longer and finer ones. Ventral to the subanal flap is a small group of 20–25 short stout bristles, with two rather larger than the rest, and 2–5 long fine bristles. In this species no bristles are hooked.

2. *Metanastes vulgivagus.*

The average width of the head capsule of a first instar larva is 2·1 mm.; of a second instar larva is 3·5 mm.; the length of a fully-fed final instar larva is about 30 mm., and the average width of the head capsule 5·5 mm.



Figs. 1-2.—*Heteronychus sanctae-helenae.* 1, Adult male fore tarsus; 2, adult female fore tarsus.

Fig. 3.—*Metanastes vulgivagus.* Head capsule of third-instar larva, showing frontal chaetotaxy.

Figs. 4-7.—*Heteronychus sanctae-helenae.* 4, Head capsule of third-instar larva, showing frontal chaetotaxy; 5, mandible, showing oval stridulating area; 6, maxilla, showing plectrum; 7, epipharynx.

The head is reddish-brown in colour, quite distinctly darker than *Heteronychus sanctae-helenae*; the coronal suture is darker than the rest of the epicranial suture (Fig. 3). On the frons there are four long bristles only (not including the 2–3 pairs between the antennal bases and the mandibular articulations) in contradistinction to the 14–20 long and short bristles on the frons of *Heteronychus sanctae-helenae.* The head is finely reticulated and deeply and closely punctate (Plate ix, fig. 1). The four points on which the two species differ in regard to the external morphology of the head are size, colour, frontal chaetotaxy and puncturation.

The distal sensory area is a curved chitinous area projecting proximally as three large teeth. The difference between the two species is obvious on comparison (Figs. 7, 8).

The subanal flap carries along the lower lip of the anus 20–25 short and long straight bristles (Fig. 10); the rest of the area is occupied by 30–35 curved (many hooked) and stout bristles, more or less evenly spaced. The longitudinal bare space, dorsal to the anus, seen in *Heteronychus sanctae-helenae*, is missing; the chaetotaxy in this region consists of mixed short and long bristles, most of which are slightly curved. Ventral to the subanal flap are 40–50 hooked stout bristles with 3 or 4 long bristles among them, and laterally long and slender slightly curved bristles.

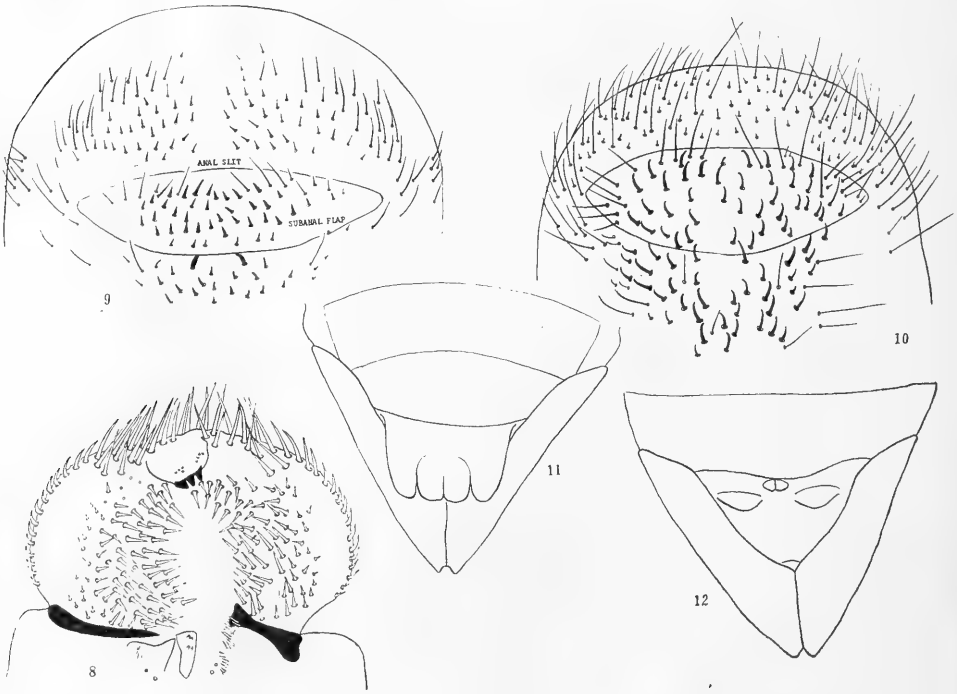


Fig. 8.—*Metanastes vulgivagus*. Epipharynx.
Fig. 9.—*Heteronychus sanctae-helenae*. Radula.
Fig. 10.—*Metanastes vulgivagus*. Radula.
Figs. 11-12.—*Heteronychus sanctae-helenae*. 11, Male pupa (terminal segments, showing genitalia); 12, female pupa.

d. Pupa.

The length of the pupa of *Heteronychus sanctae-helenae* is approximately 15 mm., of *Metanastes vulgivagus* is approximately 20 mm. In both species the pupa is exarate, the typical form of the Coleoptera, and is capable of abdominal movement only. When the larval skin is first cast off, the pupa is a uniform pale yellow, but before emergence of the adult the pronotum, head, legs and terminal abdominal segments become reddish-brown in colour. At this time the organization of the adult form is distinctly visible through the pupal integument. Male and

female pupae are easily differentiated by the general shape, the male (Fig. 11) as a rule with a more elongate and slender abdomen than the female (Fig. 12), by the fore tarsus, and by the genitalia. The fore tarsus of the male is much thicker and shorter than that of the female, because of the deformed tarsus of the adult male. The genitalia of the male are clearly seen with the naked eye at the end of the abdomen. At the time of emergence the elytra are pale, and darkening of the whole body occupies a considerable time. The adult, in fact, remains reddish-brown for some days, and while in this stage may easily be mistaken for a different species.

Summary.

In spite of the apparent close resemblance between *Heteronychus sanctae-helenae* and *Metanastes vulgivagus*, both in appearance and habits, in the two destructive stages, the larva and the adult, these species are readily distinguished by their external morphology. Since damage can only be caused when either the larvae or the adults are active, it is actually sufficient to possess knowledge only of differential diagnostic characters for these stages. Such characters have been described. It is considered that the morphological section of this paper is the more important, and it is hoped that the work will be in the future extended to include other common economic species of Scarabaeidae. In parts the morphological description of the larvae is deliberately made general, so that it is applicable to the family as a whole—relevant to this object. The discussion of the biology of *Metanastes vulgivagus* and *Heteronychus sanctae-helenae* was included for the sake of completeness, since bionomical work on both species has previously been carried out and the results published.

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EXPLANATION OF PLATE IX.

1.—*Metanastes vulgivagus*. Head capsule of third-instar larva, showing puncturation.
2.—*Heteronychus sanctae-helenae*. Head capsule of third-instar larva, head smooth.
3.—*Heteronychus sanctae-helenae*. Epipharynx.
4.—*Metanastes vulgivagus*. Epipharynx.

THE GEOMORPHOLOGY OF THE HUNTER RIVER DISTRICT, N.S.W.

By C. A. Sussmilch.

(Plate x; three Text-figures.)

[Read 29th May, 1940.]

It is proposed in this paper to describe the geomorphology of that part of eastern New South Wales which is drained by the Hunter River and its tributaries; this river is one of the larger streams flowing from the eastern side of the Main Divide to the coast, and the position of its watershed is indicated on the map (Pl. x). This area, which is one of the most important industrial and pastoral regions of the State, is relatively low, most of it being under 2000 feet in altitude, although limited areas along some of its margins considerably exceed this amount; the regions to the north and south of it are, however, much higher. To the north lies the New England Tableland varying from 3000 to upwards of 5000 feet in altitude, while to the south lies the Central or Blue Mountain Tableland ranging from 3000 to 4000 feet in altitude.

No previous attempt has been made to give a detailed description of the physiography of this region as a whole, but various writers have made reference to some of the physiographical features of certain parts of it, usually in connection with a description of the geology. The first important reference was that by E. C. Andrews (1903), who gave a brief description of some of the features of the Hunter River Valley; in a later paper (1910) he suggested that the scarps along the western and southern sides of the Barrington Tableland are fault-scarps. In 1912 the same writer published a description of a relief model of New England which included the northern portion of the Hunter River Valley; and later he (1914) expressed the opinion that the Main Divide in the Hunter River area had had a tectonic origin, without, however, quoting any detailed evidence in support of this view. The present writer (1914) put forward a similar view.

T. Griffith Taylor (1906), dealing with the western part of the Hunter River drainage area, ascribed its relatively low elevation, as compared with the higher elevation of the tablelands immediately to the north and south of it, to the relatively easy and rapid cutting down of the weak coal measures by the Goulburn River and its tributaries; he was evidently of the opinion that the whole of the surface of this region was occupied by the Upper Coal Measures of Permian age. He stated that "it is possible that the New England massif originally extended towards the south and joined the Blue Mountains massif with but little lowering of the 3000 ft. contour. There is little doubt at any rate as to the action of the Hunter and its tributaries in materially reducing the level of this region and thus leading to the diversities in temperature and rainfall." As will be shown later, his views are not supported by the evidence. In a later paper Taylor (1911) again referred to this area and suggested that all that part of the Hunter River system west of Singleton at one time flowed westward and formed a part of the Macquarie River system.

The present writer (1920) gave a brief description of some of the physiographical features of the Hunter River Valley. W. R. Browne (1924) described some of the physiographical features of the Upper Hunter River district, and G. D. Osborne (1929) described the physiography of a relatively narrow belt of country extending from Scone eastward to Raymond Terrace. J. A. Dulhunty (1938) made reference to some of the physiographical features of the Wollar District.

Subdivisions.

For purposes of description it will be convenient to divide the area under consideration into the following divisions:

A. The Lower Hunter Tableland .. .. General altitude 1400 to 1500 feet
B. The Barrington Tableland .. .. .. General altitude 4000 to 5000 feet
C. The Upper Hunter Tableland .. .. General altitude 2200 to 3300 feet
D. The Goulburn River Tableland .. .. General altitude 1450 to 2200 feet
E. The Blue Mountain Tableland .. .. General altitude 2000 to 4000 feet

This subdivision is based primarily on differences in altitude, and to a less extent on differences in geological structure; geologically the region falls naturally into two divisions. In the north-eastern part, which comprises the whole of the Barrington and Upper Hunter Tablelands together with most of that part of the Lower Hunter Tableland lying to the north of the Hunter River, the underlying geological formations consist dominantly of Devonian and Carboniferous strata with a quite subordinate extent of Permian strata; all of these formations are strongly folded, and upon their truncated edges in many places lie horizontal flows of Tertiary basalt, particularly in the northern section. Throughout the remaining portion of the Hunter River drainage area the geological formations are, for the most part, quite unfolded, and consist of a thick series of Mesozoic strata, resting, for the most part conformably, upon an underlying thick series of Permian strata, the latter extending down to and below sea-level; such limited folding of the Permian strata as occurs in this section soon flattens out and disappears southward and westward. Resting in places upon the Mesozoic strata, with a definite but not very pronounced unconformity, are a series of Tertiary basalt flows; these are particularly well developed in the north-western part of the area.

The physiographic features of each of the subdivisions listed above will now be described in turn.

A. The Lower Hunter Tableland.

This portion of the drainage area of the Hunter River extends from the seacoast westward to Muswellbrook, a distance of about 60 miles, where it joins the Goulburn River Tableland. Northward it extends to the Barrington and Upper Hunter Tablelands, while southward it extends to and continues beyond the southern boundary of the Hunter River watershed. This tableland has been very completely dissected since its uplift, and but little of the original surface now remains; the general altitude of its surface, as indicated by the heights of the various trigonometrical stations which lie upon it, is about 1400–1500 feet; in the southern area the following trigonometrical stations occur; Heaton (1582 feet), Myall (1550 feet), Quarrybylong (1411 feet), Milfield (1450 feet), Barraba (1694 feet), and Mount Warrawolong (2020 feet); near its western margin are Ogilvie (1518 feet), and Arthur (1567 feet), both near Muswellbrook; and in the northern section Mount Tangorin (1532 feet), George (1466 feet), and Richardson (1536 feet). The close correspondence in altitude of all of these high points (with

the exception of Mount Warrawolong) over such a wide area, nearly 3000 square miles, is strong presumptive evidence that the original altitude of the tableland was approximately 1400–1500 feet. Some of these appear to project slightly, but not notably above the general tableland level. Mount Warrawolong is an isolated basalt-capped peak, and its greater altitude is due to the thickness of the basalt capping. T. W. E. David (1907) stated that basalt (dolerite) extends from the summit down to an altitude of 1320 feet. There is, however, one section of this tableland—the Broken Back Range lying just to the west of the town of Cessnock—definitely above the general 1400–1500-foot level; this is not an isolated peak like Mount Warrawolong, but is a narrow tableland extending from Wollombi northward nearly to Singleton, and increasing in altitude northward, reaching at its northern end an elevation of 1925 feet. Like the surrounding lower tableland, it is capped with a thick series of Triassic sandstones which are, however, no thicker here than in the surrounding lower areas, and near Wollombi these massive sandstones are seen to be definitely tilted downward towards the lower level lying to the west. The Broken Back Range therefore appears to be a part of the tableland which at the time of uplift was warped upwards above its surroundings. It is interesting to note that this upwarped area corresponds closely in position and trend to the Lochinvar Anticline in which the Permian strata were notably elevated above their surroundings when undergoing folding towards the close of the Permian Period.

The Hunter River Valley traverses the Lower Hunter Tableland from west to east, and divides it into two sections, which have very different geological structures; in the southern section the tableland is capped by a series of massive sandstones, grits and conglomerates ranging up to 1000 feet in thickness, and these rest upon a thick series of Permian strata consisting mainly of interbedded shales and sandstones. The Triassic strata are for the most part quite unfolded and are nearly horizontal, with but a slight dip to the south; the Permian strata in the northern part of this section adjacent to the Hunter River are definitely folded, but southward the folds soon flatten out, and the strata become nearly horizontal. In the northern section, on the other hand, the strata consist dominantly of highly-folded Devonian and Carboniferous strata with small areas of folded Permian strata along the southern margin. In both northern and southern sections some small patches of Tertiary basalt occur on the tableland surface, apparently residuals of one-time extensive lava flows.

The present valley of the Lower Hunter River is located approximately along the line of junction between the highly-folded Carboniferous and Devonian strata of the northern area and the practically unfolded Permian and Triassic strata of the southern area, and here a very wide mature valley has been developed. The Permian strata which occur at base-level along this part of the Hunter River form a very weak structure, and once the overlying resistant Triassic sandstones had been cut through, rapid widening of the valley took place, particularly along its southern side, not only along the course of the Hunter River itself, but also along the courses of all of its southern tributaries, giving wide, nearly flat-floored valleys, along whose sides are high, almost vertical escarpments of the Triassic sandstones. Southwards these flat-floored valleys head into narrow gorges cut in the Triassic sandstones.

In the northern section, in the highly folded formations, the rivers, such as the Paterson and Williams, follow the general strike of the strata and have developed relatively narrow sub-parallel valleys separated from one another by sharp, narrow hog-back ridges.

The fact that the 1400–1500-foot level of the original tableland extended uniformly through both the folded and unfolded strata of the whole of the Lower Hunter Tableland area suggests that this surface, before it was uplifted, was a peneplain.

B. THE BARRINGTON TABLELAND.

This tableland, which lies to the north of the eastern part of the Lower Hunter Tableland just described, has an altitude varying from 4000 to 5000 feet; this is the highest part of the Hunter River watershed; it is really a part of the New England Tableland which projects southward into the Hunter River Valley. It is highest along its southern margin; there known as the Barrington Tops, where its general altitude is 4900 feet, with some few points, such as Carey's Peak, slightly exceeding 5000 feet in altitude. The northern portion, known locally as the Hunter Tops and Thunderbolt Tops, is not so high, ranging from 4000 to 4500 feet in height. Only the southern and western margins of the Barrington Tableland are drained by the Hunter River and its tributaries, the major part of it falling within the watershed of the Manning River. It should be noted that this high tableland, one of the highest regions in New South Wales, does not lie on the Main Divide, but is located to the east of it and lies entirely within the watersheds of eastern river systems.

The Barrington Tableland is very deeply dissected, particularly so along its eastern margin, but in the south-western section there remains a considerable portion, some 60 square miles or more in area, which is still practically unaffected by the activities of the present cycle of erosion and which displays a remnant of the Tertiary land surface as it existed there before the tableland was uplifted. The general level surface of the tableland of this area is modified by the presence on it of a series of broad mature valleys sunk below the tableland and from 400 to 600 feet deep; such mature valleys are particularly well developed about the headwaters of the Barrington River, Upper Manning (Gummi) River, Polblue Creek, and Moonan Brook, the two last-named streams being tributaries of the Upper Hunter River. The maturity of the topography of the country about the headwaters of these streams is in marked contrast with what is found a few miles downstream, where these rivers suddenly plunge into profound and almost impassable gorges 3000 feet or more in depth.

The Barrington Tableland consists of a thick series of highly folded strata of Devonian and Carboniferous age, associated with which are some extensive granite intrusions; resting unconformably upon the truncated edges of these formations there is a series of horizontal basaltic lava flows of Tertiary age. This volcanic series caps the whole of the tableland, but in the upland valleys just described, the lava flows have been cut through and the much older intrusive granites exposed. These granite outcrops have not been surveyed in detail, but in an unpublished map prepared by the surveyors of the Lands Department their boundaries are shown approximately and the figures given indicate the altitude of the contact of basalts and the granites to be a fairly uniform one varying from 4200 to 4500 feet. These conditions suggest that throughout this area of about 60 square miles the surface of the older rocks upon which the basalts were deposited was a peneplain with no great relief, and that the volcanic series as a whole do not much exceed 700 feet in thickness. Along the western margin of the Barrington Tableland, however, different conditions are found, and from this region Dr. G. D. Osborne kindly supplied to the writer the following information regarding the altitude of the base of the volcanic series as well as its thickness:

Locality.	Altitude of Base of Volcanic Series.	Thickness of Volcanic Series.
Mt. Royal	2800 – 2900 feet	964 feet
Mt. Cockcrow	2900 – 3000 feet	1550 feet
Mt. Woolomin	2800 – 3300 feet	1670 feet +
Stewart's Brook	3000 feet	
Moonan Brook	3100 feet	
Road, Moonan to Wharton's Mill	3300 feet	700 feet

All these observations were made on steep hill-sides where, owing to the tendency of basalt boulders to drift down the slope, it is difficult to locate accurately the true base of the volcanic series, so that the correspondences in the figures from these six localities may be even closer than the figures actually indicate, and it appears to be reasonable therefore to accept a general average of about 3000 feet as the altitude here of the base of the volcanic series. These six localities lie along an approximately north-south line some twenty-four miles in length and at each of them the volcanic series rests upon the truncated edges of folded Devonian and Carboniferous strata. At Murrurundi, some 30 miles westward of the northern end of this line, the writer has determined the altitude of the base of the volcanic series to be also at 3000 feet, and here, too, they rest upon the truncated ends of folded Carboniferous strata. These facts suggest that along the whole of the western margin of the Barrington Tableland, and thence along the southern margin of the New England Tableland to Murrurundi, the Tertiary volcanic series rests upon a peneplained surface of no great relief, and that this feature, together with the base of the volcanic series, now stands at an altitude of approximately 3000 feet. This is some 1200 to 1500 feet lower than the altitude of the suggested possible peneplain surface in the granite region immediately to the east; such a difference in altitude can be explained in either of two ways: (*a*) that a post-basalt fault or a monoclinal fold with an approximate north-south trend separates the two areas, or (*b*) that the granite outcrops in the eastern area are not parts of a peneplained surface, but are the tops of one or more granite residuals rising some 1200 to 1500 feet above a peneplained surface at their bases, and subsequently submerged under the Tertiary volcanic series, which in that case would need to be upwards of 1900 feet in thickness. The absence of any surface features, such as a fault scarp between the two regions; the great thickness of the volcanic series at Mt. Woolomin and other places already referred to; and the further fact that this mountain is nearly as high as the highest parts of the Barrington Tableland, support the latter view. A final decision must await a more detailed geological survey of the whole region, but as this region is very rugged, heavily timbered and rather inaccessible, many years will probably pass before a detailed geological map will become available.

The southern margin of the Barrington Tableland where it joins the Lower Hunter Tableland is marked by a magnificent scarp trending almost due east and west, and giving a drop of more than 3000 feet from the higher to the lower tableland. This scarp displays all the characteristic features of a true fault scarp, and was diagnosed as such by E. C. Andrews in 1910. In ascending this scarp by the bridle track (the only one available) which follows the divide between the Williams and Paterson Rivers, basalt is first met at an altitude of about 2200 feet, and this rock *appears* to outcrop continuously from there to the summit of the tableland at Carey's Peak (about 5000 feet in altitude), giving an apparent thickness to the volcanic series of about 2800 feet. Detailed mapping might, however, reveal breaks in this apparently continuous outcrop, in which the older rock outcrops are concealed by basalt talus; even without such visible breaks step-faulting

could have brought about an apparent increase in the true thickness of the basalt. The topography of this scarp suggests that the Barrington Tableland does not break off to the south in one sheer drop, but that there is a series of steps and treads; there appears to be a well-marked bench some miles in width at an altitude of about 2200 feet, and a second well-marked bench some 2½ miles wide also occurs at an elevation of about 3000 feet. It is interesting to note that the first bench corresponds in height (2200 feet) with the surface of the southern part of the adjoining Upper Hunter Tableland, to be described in the next section, while the second bench, that at 3000 feet, corresponds in height to the base of the basalts along the western side of the Barrington Tableland as already described. These benches have, of course, been very much dissected, and partly removed during the present cycle by the erosive activities of the present-day streams draining the southern margin of the tableland. These streams all flow in a southerly direction, that is directly away from the scarp and not parallel to it.

The features just described suggest the presence of at least two normal faults, one from the 3000-foot to the 2200-foot level, with a throw to the south of 800 feet, and a second from the 2200-foot level to the 1500-foot level of the Lower Hunter Tableland, with a throw of about 700 feet; as has been pointed out previously, basalt occurs also, but to a very limited extent, on the surface of the lower 1500-foot tableland. The geological proof of the existence of these suggested faults will only become possible following a detailed geological mapping of this area, but the evidence now available, both physiographical and geological, very strongly supports E. C. Andrews' view that this great Barrington scarp is a true tectonic scarp; monoclinal folding or sharp warping could also, of course, have produced a somewhat similar feature, but this would not alter the view that this great scarp is primarily a tectonic one and not an erosional one. The western scarp of this tableland will be described in the next section.

C. THE UPPER HUNTER TABLELAND.

Lying immediately to the west of the Barrington Tableland is a lower tableland which is drained for the most part by the Upper Hunter River and its tributaries, and which may therefore be suitably called the Upper Hunter Tableland. In its southern part this tableland has an altitude of 2000 to 2200 feet, as indicated by the height of the trigonometrical stations occurring there, such as Mount Dyrring (2153 feet), Mount Wells (1941 feet), Kangaroo Mountain (2307 feet), Bell Mountain (2240 feet), and Scone Mountain (2200 feet); in addition the main ridges of this area also rise to an approximately similar height. Northwards of Scone Mountain the general altitude increases and reaches some 3000 to 3300 feet, where it joins on to the New England Tableland.

The geological structure of this region is identical with that of the Barrington Tableland as just described, and consists of folded Devonian and Carboniferous strata, upon whose truncated edges lie in places horizontal Tertiary basalts. At Scone Mountain these basalts are less than 200 feet in thickness, but in the northern area they are considerably thicker. It is probable that the Tertiary volcanic series originally covered much of the original surface of this tableland, but the very complete dissection which it has suffered since its uplift has brought about the removal of the volcanic series over most of the area, particularly so in the southern section. The details of the nature of the dissection of this area have already been described in some detail by Browne (1924), and need not therefore be referred to further here.

Along its eastern margin the Upper Hunter Tableland abuts against the great western scarp of the Barrington Tableland, and that this scarp is a fault scarp was first suggested by E. C. Andrews in 1910; there is definite geological and physiographical evidence in support of this view, as may be seen from the section given in Text-figure 1. Along the western margin of the Barrington Tableland, as has already been shown, the base of the Tertiary basalts, together with the peneplained surface of older rocks upon which they rest, stands at a present elevation of about 3000 feet, whereas in the Upper Hunter Tableland immediately to the west the same features stand at an elevation of about 2000–2200 feet, and the drop from the higher to the lower level is a very abrupt one. A normal fault (or faults) with a throw to the west of about 800–1000 feet would explain this feature, as would also a steep monoclinal fold. As the Devonian and Carboniferous strata of this region have not yet been geologically mapped in detail, they afford no present evidence in favour of faulting, but the author has seen evidence of faulting in these older rocks at Stewart's Brook, just where it crosses this suggested line of late Tertiary faulting; the evidence here does not, however, date the faulting, except that it is post-Carboniferous.

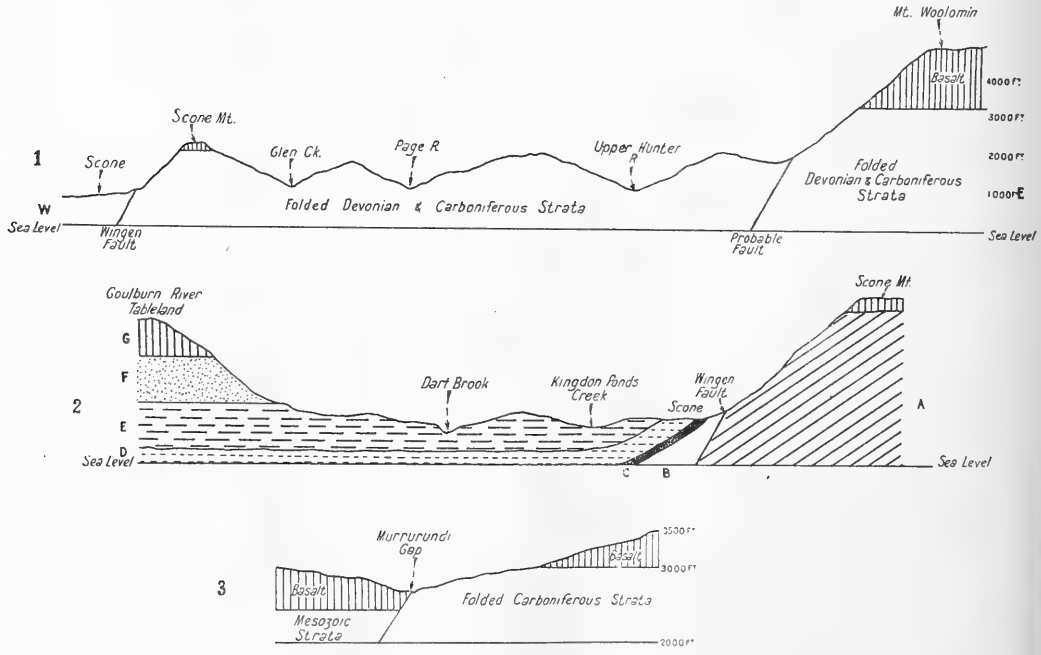
The trend of this scarp is approximately meridional and corresponds, but only approximately, to the strike of the strata, and this raises the question as to whether the scarp could be explained as being due to differential erosion; the strata in the two adjoining blocks are, however, of similar age and character, and are equally resistant to erosion; furthermore, the rivers draining this area do not follow either the trend of the scarp or the direction of strike of the strata, their direction of flow ranging from west to south-west, that is, they flow directly away from the scarp, and, as has already been pointed out by Browne (1924), they cut across harder and weaker formations alike; the conditions therefore do not support an origin due to differential erosion, and the whole of the evidence strongly supports the view that this is a tectonic scarp.

The original position of this scarp lies at the western face of Mount Woolomin, where part of it, somewhat modified, of course, still remains, but the scarp as a whole has been much dissected since it was produced, as a result of which it has, both to the north and to the south of Mount Woolomin, retreated some distance to the east of its original position.

Southward, the Upper Hunter Tableland overlaps the Barrington Tableland and here it adjoins the northern portion of the Lower Hunter Tableland, already described; this junction has not been investigated by the writer, but G. D. Osborne (1929) has expressed the view that there is no sharp break between the two, but that the higher region is warped down easterly to the lower.

The Upper Hunter Tableland is also bounded by a fault-scarp along its western side as may be seen from the geological section given in Text-figure 2; it will be obvious from this section that the Mesozoic strata together with the overlying Tertiary basalts of the Goulburn River Tableland must have, at one time, extended eastwards across the present wide valley of Kingdon Ponds Creek to this scarp, and have there come into unconformable contact with the highly-folded Carboniferous strata, and that the junction was a faulted one; further to the north, at Murrurundi, this faulted contact still exists. This line of faulting has been traced by Browne (1924) from Scone to Wingen and called by him the Wingen Fault; he considered it to be of Tertiary age; southward from Scone to Segenhoe where it cuts off the Hunter overthrust of Epi-Permian age, it has been mapped by G. D. Osborne. The Wingen Fault is obviously a normal one with a downthrow

to the west and, using the altitude of the base of the basalts as a datum (2000 feet at Scone Mt. in the higher tableland and 1450 feet in the lower tableland), it must have a throw of about 550 feet. From Segenhoe to Wingen this fault has an approximately meridional trend and follows the junction between the Permian and Carboniferous strata, but its position north from Wingen has not yet been definitely determined. North of Wingen the Permian-Carboniferous junction swings to the north-east and, after following this direction for some miles, swings around to almost due west to Murrurundi; here it crosses the Main Divide and north of this point it appears to change its course to a north-north-westerly direction along the western margin of the New England Tableland. Within this big easterly bend from Wingen to Murrurundi the whole of the Permian formations, including the Lower Coal Measures, the Upper Marine Series and the Upper Coal Measures, are strongly folded, and no Mesozoic strata now occur there. Until the district between Wingen and Murrurundi has been surveyed in detail it will not be possible to say whether the Wingen Fault follows this great bend or whether it takes a more direct course through Blandford to Murrurundi. There is some evidence in favour of the latter view because at the junction of the Timor Road with the main road from Wingen to Murrurundi (Portion 60, Parish of Murulla) the dip of the Upper Coal Measures is almost vertical; Mr. C. J. Ivin of Murrurundi



Text-fig. 1.—Diagrammatic Section across Upper Hunter Tableland. Scales: Horizontal, 1 inch = 5 miles; Vertical, 1 inch = 5000 feet.

Text-fig. 2.—Section from Goulburn River Tableland to Scone Mountain. Scales: Horizontal, 1 inch = 2·5 mile; Vertical, 1 inch = 250 feet.

A, Kuttung Series (Carboniferous); B, Lower Marine Series; C, Lower Coal Measures; D, Upper Marine Series; E, Upper Coal Measures; F, Triassic Sandstones and Conglomerates; G, Tertiary Basalt.

Text-fig. 3.—Sketch Section at the Murrurundi Gap. (Not to scale.)

has informed me that similar conditions were also found in a well-hole on Harben Vale Station; both of these localities lie on the line of the general strike of the Wingen Fault. Immediately to the north of these localities the country is fairly flat and covered with soil and alluvium, and consequently the geological structure is obscure. A section across the fault where it crosses the Main Divide at Murrurundi is given in Text-figure 3; here both the Mesozoic strata and the overlying Tertiary volcanic series come into direct contact with the Carboniferous strata along the line of fault, and every one of the formations mentioned shows evidence of the faulting movement; the Carboniferous strata are sheared and strongly jointed adjacent to the fault plane, the Mesozoic strata are strongly tilted and in one place are nearly vertical, whereas a few chains away they are practically horizontal; similarly the Tertiary lava flows close to the fault plane are tilted and dip away from it at an angle of about 25°. Tertiary basalts occur on both sides of the fault, resting upon the folded Carboniferous strata on the upthrow side and on the unfolded Mesozoic strata on the downthrow side, with a difference in the elevation of their base of about 550 feet, giving a similar amount of throw of the fault here to that indicated by the evidence at Scone. The evidence at Murrurundi shows conclusively that the Tertiary basalts have been displaced by the faulting and that the age of the faulting is therefore post-basaltic, that is, late Tertiary. At Murrurundi, and for some miles eastward from there, this fault has a nearly east-west trend; as will be shown in the next section, there is also a probable line of faulting (or monoclinal folding) extending westward from Murrurundi along the northern face of the Liverpool Range; it is possible therefore that these two features are continuous and that the Murrurundi fault has displaced the Wingen fault, and that the fault which extends north-north-west from the northern side of the Murrurundi Gap is a displaced part of the Wingen fault; these possibilities, however, need further investigation.

The southern and south-western margin of the Upper Hunter Tableland from Muswellbrook to Singleton also follows the junction between the Carboniferous and Permian strata which in this region is marked by an overthrust fault (the Hunter Overthrust); H. G. Raggatt (1929) suggested an early Tertiary age for this fault, but later Carey and Osborne (1938) have expressed the opinion that it is of late Permian age. It is improbable that any movement took place on it as late as the close of the Tertiary period, when this tableland was uplifted. The Upper Hunter Tableland is in this region separated from the Lower Hunter Tableland lying to the south of it by the very wide mature valley of the Hunter River, here some 10 to 15 miles in width, so that it is now difficult to determine what the physiographic relationship of these two tablelands was before the valley was eroded, but the fact that the present most northerly projection of the Lower Hunter Tableland in this area (the Broken Back Range) has an altitude of 1925 feet, which closely approaches the height of the southern part of the Upper Hunter Tableland (2200 feet), suggests that the two were originally joined by a warped surface.

D. THE GOULBURN RIVER TABLELAND.

This comprises the whole of the western part of the Hunter River drainage area—an area of about 3000 square miles; along its eastern side it adjoins the Upper Hunter and Lower Hunter Tablelands already described, but it is today actually separated from them by the wide mature valleys of the Hunter River and Kingdon Ponds Creek; on all other sides it extends to the Main Divide. A glance at a map of New South Wales will show that the general meridional trend

of the Main Divide of this State is interrupted at the head of the Upper Hunter River by a marked westerly bend; this bend starts at the southern margin of the New England Tableland where, not far from the head of the Upper Hunter River, the Main Divide suddenly turns westward and continues in that direction for some sixty miles, this part of its course being known as the Liverpool Range. The Main Divide then turns southward, maintaining this direction for a distance of sixty miles, and along this section it is so inconspicuous that it has not received any special name; a few miles south of Ulan it again turns suddenly, this time to the south-east, and continues in this direction for about fifty miles, and then resumes its original north-south course. Nearly the whole of the region included in this great westerly bend of the Main Divide is drained by the Goulburn River and its tributaries, and it seems suitable therefore to refer to it as the Goulburn River Tableland.

The Goulburn River traverses this region approximately from west to east and divides it into two unequal parts, a larger northern part which may for convenience be referred to as the Merriwa section, and a smaller southern part which may be referred to as the Bylong section. In both sections the tableland was warped and tilted during uplift, but in opposite directions, the Merriwa section having a gentle but quite definite tilt from north to south, whereas the Bylong section has a much steeper tilt from south to north. There is also in addition a quite definite warping from west to east, which is most marked along the western margin adjacent to the Main Divide. As a result of this warping the altitude of the tableland as a whole varies considerably; it is lowest where the Goulburn River leaves it at its eastern margin, and here the altitude is about 1450 feet; from this point it rises southward to an altitude of 3000 feet, westward to an altitude of 1900 feet and northward to an altitude of about 2200 feet; the highest parts are therefore along its southern, western and northern margins.

The geological structure of the Goulburn River Tableland is similar throughout the whole of its extent, and includes the following formations:

1. The Tertiary Volcanic Series, mainly basalt flows.
2. The Jurassic System—(*a*) sandstones and conglomerates up to 300 feet in thickness; (*b*) the Comiala Shales up to 210 feet in thickness.
3. The Triassic System.
   The Wollar Sandstones up to 650 feet.
4. The Permian System.
   The Upper Coal Measures up to 500 feet in thickness.

The Comiala Shales appear to be limited in their occurrence to the Merriwa section of the tableland.

The above details have been taken from Dulhunty's description (1938) of the geology of the central and northern parts of the region. In addition, the Upper Marine Series have been seen by the writer to outcrop in the lower part of the Bylong valley. A number of geological sections and a geological map of the south-western part of the area have been published by L. J. Jones; his sections show very clearly the marked warping of the tableland in this region. The information published by these observers, together with the author's own observations over very considerable parts of the area, shows that throughout the whole of the Goulburn River Tableland the geological structure is essentially the same.

The volcanic series is quite unfolded and rests unconformably upon the underlying older formations; but its occurrence is limited for the most part to the region lying to the north of the Goulburn River. The Jurassic, Triassic and

Permian formations are apparently quite conformable with one another, and are in general not folded; Dulhunty (1938) has shown, however, that some very gentle folding has taken place in them in the Wollar District; he has shown also that all of these formations had been gently tilted and eroded in pre-basalt times and that the surface upon which the volcanic series rests is a peneplained surface cut in the older rocks; the whole of the formations, as well as the peneplain itself, were subsequently tilted by the warping which accompanied the upward movement (Kosciusko Uplift) which produced the present tablelands. The Mesozoic formations, consisting as they do mainly of sandstones and conglomerates, are very resistant to weathering and erosion, and display steep escarpments where they are exposed in the valley sides; the Upper Coal Measures, on the other hand, consisting mainly of soft shales, are a relatively weak feature and have allowed considerable benching in the central part of the area; over much of the Goulburn River Tableland, however, particularly in the Merriwa section, dissection has not yet exposed the Upper Coal Measures, the surface being still occupied, either by Mesozoic sandstones or by the overlying volcanic series.

Although the Merriwa and Bylong sections of the Goulburn River Tableland have a similar geological structure and similar physiographic histories it will be convenient to describe each separately.

1. *The Merriwa Section.*—As already pointed out, this region lies to the north of the Goulburn River; at its south-eastern margin it has an altitude of from 1400 to 1500 feet, and from here the surface rises northward to the foot of the Liverpool Range, which marks the northern margin, and here the altitude is about 2200 feet. As the volcanic series thickens in a northerly direction the best measure of the amount of tilting of this section of the tableland is given by the underlying sedimentary formations, and for this purpose it will be convenient to take the base of the Mesozoic formations; at Sandy Hollow, at the southern margin, this feature stands at an altitude of 450 feet, whereas at Mount Murulla on the northern margin it stands at an altitude of 1250 feet, a rise of 800 feet in about 36 miles.

Throughout most of the Merriwa section of the tableland the surface is occupied by the volcanic series, but towards its southern margin these thin out and the underlying Mesozoic sandstones are exposed at the surface, particularly so in the bases of the river valleys. An examination of the contact of the volcanic series with the peneplain surface upon which it rests shows that just prior to the outpouring of the basalts, a series of shallow valleys some 300 feet deep had been incised into its surface, and the basalts not only filled many of these valleys but overflowed and spread out over the surface of the peneplain itself. Upon the cessation of the volcanic action, valley development was resumed, with the production of an extensive series of wide mature valleys some 300 feet deep cut alike in the basalts and in the older rocks. These Tertiary valleys (the "upland valleys" of E. C. Andrews) still survive over extensive areas not yet affected by the dissection of the present cycle of erosion. The headwaters of the Goulburn River itself, for example, still lie in one of these Tertiary valleys; at Ulan, where the Goulburn River is flowing northward parallel to and not far east of the Main Divide, it lies in a valley some 3 miles wide, some 300 feet below the tableland surface; its floor is heavily aggraded, and the Mesozoic sandstones which cap the ridges bounding it are covered by a thick mantle of soil; Browne has studied the character of this soil and considers it to be of Tertiary age. The northerly tributaries of the Goulburn River such as Munmurra River and Krui River lie

also in similar mature valleys and all of these streams wind sluggishly over their aggraded valley floors, and no downward erosion is at present taking place. In his description of part of this area Dulhunty (1938, p. 308) states that "the peneplain surface has been fairly extensively dissected by the Goulburn River and its tributaries, producing a drainage system which consists mainly of wide shallow valleys exhibiting a considerable degree, and in places an advanced stage, of maturity". These "upland valleys" of the Goulburn River Tableland are quite similar to those which occur in many other parts of New South Wales on similar undissected tableland remnants. The cycle of erosion which produced them was interrupted by the Kosciusko uplift which uplifted the existing tablelands; this uplift rejuvenated the streams and as a result the Goulburn River over much of its course has now cut its channel well below the level of the Tertiary "upland valleys".

Along the northern margin of the Merriwa section stands the Liverpool Range, whose higher peaks range from 3000 to 3500 feet in altitude; this great altitude is due to the great thickness of the volcanic series along this line. The Mesozoic strata continue northward under the volcanic series, and at Warrah Station on the northern side of the range the author found the junction of the two formations to be at an altitude of approximately 1300 feet; at Mount Murulla on the southern side of the Liverpool Range this junction stands at an elevation of approximately 2200 feet, that is, higher by about 900 feet; either faulting or steep warping, or a combination of both, with a downthrow to the north, must have taken place along this east-west line during the Kosciusko uplift; it is obvious therefore that this part of the Main Divide (Liverpool Range) has had a tectonic origin. The great thickness of the basalts (1300 feet or more) along this same line, with their rapid thinning both to the north and to the south, suggests that this was a line of active vulcanism during the Tertiary volcanic epoch, from which basaltic lava flows were poured out, flooding the country northward and southward for many miles.

To the west of the Merriwa section of the Goulburn River Tableland lies the Coolah Tableland which is similar to it both geologically and physiographically; it differs, however, in being notably higher; at Cassilis, which lies just to the east of the Main Divide, the general altitude of the Goulburn River Tableland is 1550 to 1600 feet, whereas immediately to the west of the Main Divide the Coolah Tableland has a general altitude of 1900 to 2000 feet, a difference of 300 to 400 feet; the ascent from the lower to the higher level, which occurs right at the Main Divide, is quite an abrupt one; no evidence of faulting has been found, and the divide here appears therefore to be a monoclinal fold with a throw to the east, possibly with some minor faulting. The Coolah Tableland, like the adjoining part of the Goulburn River Tableland, has a definite southerly warp. Rising above the general level of the Goulburn River Tableland in the south-eastern corner of the Merriwa section is Mount Dangar, which is 2232 feet in altitude; it rises notably above its surroundings on all sides. The author has had no opportunity of ascending this mountain, but it has been described by the late J. E. Carne, who stated that it is capped by a layer of basalt 480 feet in thickness. As the general level of the tableland at its base is not more than 1450 feet, its height above tableland level is about 782 feet; therefore, if J. E. Carne's figures are correct, the lower 302 feet of this mountain must consist of Mesozoic sandstones, and the mountain itself must be a residual of the older tableland out of which the present peneplain was eroded; similar basalt-capped residuals are fairly numerous in the Blue Mountain Tableland immediately to the south.

2. *The Bylong Section.*—This extends southward from the Goulburn River to the Blue Mt. Tableland, a distance varying from about 16 miles on its western margin to about 24 miles on its eastern margin. To the west it adjoins the Mudgee-Gulgong Tableland, and from there extends eastward to Baerami Creek, a distance of about 48 miles. Its surface has a very marked tilt from south to north. The altitude along its northern margin is about 1450 feet (but rising somewhat westward), and it rises rapidly southward, reaching an altitude of 3000 feet where it joins the Blue Mountain Tableland. Its geological structure is similar to that of the Merriwa section, excepting that the Tertiary basalts are practically absent, the surface of the tableland consisting of massive Mesozoic sandstones.

Owing to the initial steeper slope of the surface of this section of the Hunter River Tableland, as compared with the Merriwa section, the streams have a much steeper grade, as a consequence of which dissection during the present cycle has proceeded much further; the steeper dip of the underlying strata has brought the weak Upper Coal Measures well above the temporary base-level (the Goulburn River channel) with the result that, as soon as these streams had cut their channels through the Mesozoic sandstone, rapid widening of the valleys took place, with the production of wide flat-floored valleys which pass upward into narrow gorges as the divide is approached.

This Pleistocene dissection of the tableland has almost completely removed the original Tertiary topography except for small areas along the western margin close to the Main Divide where some of the original peneplain surface with its upland valleys still survives. The Permian-Mesozoic formations along the western margin end at the Main Divide, and immediately to the west and at a similar altitude an exactly similar topography of peneplain and upland valleys exists on the Mudgee–Gulgong Tableland, where the underlying formations are entirely different, consisting of highly-folded Lower Palaeozoic strata with extensive granite intrusions. The Main Divide here is so inconspicuous that in travelling from Ulan westward to Mudgee it is difficult to realize just where the divide is and the monoclinal fold previously described as occurring further to the north along the Main Divide between Cassilis and Coolah has here become a mere warping of the tableland toward the east.

The southern margin of the Bylong Section where it adjoins the Blue Mountain Tableland is marked by a line of sharp warping or faulting, or a combination of both. At Solomon's Gap on the Rylstone–Bylong Road, on the Blue Mountain Tableland, the base of the Triassic sandstones is at an altitude of about 2300 feet, whereas at The Gulf some few miles to the north, the base of the same formation is at an altitude of 1700 feet, and at this point both the Triassic sandstones and the underlying coal measures show evidence of faulting; a throw of about 600 feet to the north is indicated. This line of faulting and warping has an approximate east-west trend and extends westward into the Mudgee District where folded Lower Palaeozoic strata have been similarly affected.

Some of the southern tributaries of the Goulburn River, notably Widdin Brook and Baerami Creek, have cut their channels southward beyond this tectonic line during the present cycle of erosion, and there has been a southerly migration of the divide there for a distance of 12 miles or more; this migration is still going on.

Taking the Goulburn River Tableland as a whole it will be seen from the description already given that its northern, western and southern boundaries are primarily of tectonic origin, and that migration of the divide as a result of headward erosion of the streams during the existing cycle of erosion has only occurred

to a very limited extent in the south-eastern corner. It is quite obvious, therefore, that the great western bend of the Main Divide here is not due, as suggested by Taylor (1906), to the erosional activities of the present-day streams in the weak Upper Coal Measures, but has resulted from differential earth movements; as already pointed out, the weak Upper Coal Measures are only exposed at the surface in this region to a very limited extent.

Along the eastern side of the Goulburn River Tableland the Hunter River and its tributary, Kingdon Ponds Creek, have developed a very wide mature valley which now completely separates this tableland from the Upper Hunter and Lower Hunter Tablelands. This valley, although running at right angles to it, is continuous with the valley of the Lower Hunter already described and has been developed under similar geological conditions; in its details it is similar in every way.

E. THE BLUE MOUNTAIN TABLELAND.

Very little of this tableland falls within the drainage area of the Hunter River, consequently only a very limited description is necessary here, a fuller description being retained for a later paper. Its altitude where it adjoins the southern margin of the Goulburn River Tableland is from 3000 to 3500 feet; eastward where it adjoins the Lower Hunter Tableland the general altitude is about 2000 feet. Its geological structure here is quite similar to that of the Goulburn River Tableland.

The Hunter River and its Valley.

The Hunter River proper is formed by the junction of two important streams, the Upper Hunter River and the Goulburn River; these unite near the village of Denman and the combined streams, conveniently referred to as the Lower Hunter, flow thence in a general easterly direction to the coast.

The Upper Hunter River and its tributaries drain nearly the whole of the Upper Hunter Tableland, the western margin of the Barrington Tableland, and the eastern margin of the Merriwa section of the Goulburn River Tableland. The Upper Hunter River itself rises in the southern margin of the New England Tableland and flows in a general south-south-west direction obliquely across the outcropping edges of folded Devonian and Carboniferous strata in a relatively narrow valley with only limited flood plains here and there; at Segenhoe, where it crosses a belt of resistant Kuttung strata in a wide gap, it flows out into the very wide mature valley already described as lying between the Goulburn River and Upper Hunter Tablelands. Its left bank tributaries such as Moonan Brook, Stewart's Brook and Rouchel Brook all rise in the western margin of the Barrington Tableland and flow almost due west across the strike of the strata to join the parent stream. One of its right bank tributaries, the Page River, has a somewhat anomalous course; this stream rises in the Liverpool Ranges immediately to the west of Murrurundi, and for some miles easterly it flows first in Mesozoic strata and then in Permian strata following the general direction of the Murrurundi fault in a wide mature valley. The weak Permian strata extend from here southward to the valley of Kingdon Ponds Creek, and this would appear to be the natural direction for this drainage system to have taken; instead, it continues south-easterly, leaves the weak Permian formation, and crosses a belt of very resistant folded Middle Carboniferous strata (Kuttung Series) in a typical gorge; at the eastern end of this gorge it enters a relatively weak belt of Lower Carboniferous strata (the Burindi Series), turns south and follows the strike of these beds in a moderately mature valley to its junction with the Upper Hunter at Segenhoe. At Scone there

is a remarkable wind gap in the belt of resistant Kuttung Series only a short distance to the west of the south-flowing Page River; the base of this gap is less than 100 feet above the river level, and contains coarse river gravels, and it appears probable that the Page River at one time flowed through this gap to join Kingdon Ponds Creek, which flows on the other side of the gap.

The only other important tributary of the Upper Hunter River on its right bank is Kingdon Ponds Creek; this stream rises on the south side of the Liverpool Range and flows from there almost due south, parallel to the Wingen Fault Scarp, to its junction with the parent stream near Aberdeen; its channel traverses the weak Upper Coal Measures in which it has developed the very wide mature valley already described as lying between the Upper Hunter and Goulburn River Tablelands; this north-south valley of Kingdon Ponds Creek joins and is continuous with the east-west valley of the Lower Hunter River.

From the description given of the Upper Hunter River and its tributaries it seems obvious that the courses of these streams had already been determined before the uplift which produced the existing tableland and that they are revived streams; Kingdon Ponds Creek may be an exception, as its course may have been determined by the Wingen Fault Scarp, subsequent to the formation of the latter.

The Goulburn River rises in the Main Divide on the far western margin of the Hunter River drainage area; from its source near Ulan it flows almost due north, parallel and close to the Main Divide for a distance of about 12 miles; it then turns east and, except for the big northerly bend near Wollar, it maintains a general easterly direction to its junction with the Upper Hunter at Denman. The origin of the northerly bend near Wollar has not been investigated by the writer, but has been discussed by Dulhunty (1938). The Goulburn River from its source to nearly as far downstream as Crowie still flows along the floor of its old Tertiary valley some 300 feet below the tableland level, as do also some of its tributaries such as Krui River and Munmurra River, but downstream from Crowie it has deepened its channel below the Tertiary "upland valley" level; for example, at its junction with Munmurra River its channel is now 550 feet below the tableland level; that is 250 feet below the "upland valley" level; still further downstream at its junction with Bylong Creek its channel is at least 600 feet below the tableland level; the figures for these two localities have been taken from Dulhunty's map. At Sandy Hollow, still farther downstream, the river bed is at a present elevation of 450 feet and is therefore about 1000 feet below the tableland level. J. A. Dulhunty's statement of "a uniform depth of the Goulburn Valley below the peneplain level which varies from 300 to 400 feet throughout the entire course of the river" is therefore not correct and is actually in conflict with the figures given on his own map.

The marked warping which accompanied the uplift of the Goulburn River Tableland as already described has brought the resistant series of Mesozoic sandstones to their lowest level in this district just where the Goulburn River crosses them above Sandy Hollow, and here their base stands at an elevation of about 450 feet; these conditions have retarded the downward cutting by the Goulburn River during the present cycle of erosion, and have correspondingly retarded the dissection of the whole of the Goulburn River Tableland above this point, with the result that the tablelands in this region are as a whole less dissected than any other part of the Hunter River drainage area. At Sandy Hollow the river has now cut through the resistant sandstone into the underlying weak coal measures and has developed a wide mature valley which eastwards merges into the wide mature

valley of the Hunter River. Upstream from Sandy Hollow, however, the river channel is still confined to a rugged gorge cut in the sandstones; similar conditions occur along the lower courses of the tributary streams in this region, such for example as Merriwa Creek. Still further upstream the base of the Mesozoic sandstones, owing to their fairly steep easterly dip, is at a much higher elevation than at Sandy Hollow, and here the Upper Coal Measures are exposed in the stream channels and valley widening is much in evidence.

On its northern side the Goulburn River receives a number of tributaries which rise on the southern side of the Liverpool Ranges and flow almost due south to meet the parent stream; Tertiary basalt flows cap most of this region, and as these thicken northwards and attain a great thickness in the Liverpool Ranges, it would seem probable that these southerly courses are consequent on the slope of the surface of the basalts and had already been determined before the tableland was uplifted. On its southern side the Goulburn River receives a number of tributaries which rise in the Blue Mountain Tableland and flow more or less due north to join the parent stream; there are practically no Tertiary lava flows in this region and their direction of flow would appear at first sight to have been determined by the northerly slope of the tableland here; but the north-south trend of such of the Tertiary "upland valleys" which survive in this area indicates that this trend may have already been determined prior to the Kosciusko Uplift. Some of these southern tributaries such as Widdin Brook, have carried their channels some miles to the south of the line of warping and faulting which marks the northern margin of the Blue Mountain Tableland, and have thus brought about a southerly migration of the Main Divide during the present cycle of erosion; this migration is still going on. The evidence in this region therefore suggests that for many of the streams draining the Goulburn River Tableland the direction of flow had already been determined in pre-Kosciusko times and that they are therefore revived streams; the position of the eastern part of the course of the Goulburn River in the "hinge" when the northerly tilt of the Bylong section of the tableland meets the southerly tilt of the Merriwa section suggests the possibility that this part of its course may have been determined by the warping which accompanied the Kosciusko Uplift.

The Hunter River (Lower Hunter), after its junction with the Goulburn River, turns eastward and follows this general direction to the coast in the wide mature valley already described. It receives a number of important tributaries on its left bank, the two most important of which are the Paterson River and the Williams River; these streams rise on the southern margin of the Barrington Tableland and flow in a general south-south-east direction, this direction of flow conforming more or less to the strike of folded Carboniferous strata of this region. The region drained by these two streams receives a more abundant and more regular rainfall than any other part of the drainage area of the Hunter River, and it will play an important part in the future water conservation of this region. Of the tributaries received by the Lower Hunter on its right bank the only one of special interest is the Wollombi Brook; this stream rises in the coast range and for the first few miles of its course flows in a general westerly direction to Wollombi, and from here it turns and flows in a general north-north-west direction to its junction with the Hunter River above Singleton. This direction of flow as compared with the easterly direction of flow of the parent stream constitutes what Taylor has called a "boat-hook" junction; the Upper Hunter also makes a similar "boat-hook" junction at Denman, and on this evidence Taylor (1911) suggested

that all of that part of the Hunter River System lying to the west of Singleton at one time flowed westward to join the Macquarie River, the adjoining stream on the western side of the present Main Divide; the author, however, does not find any evidence in support of this view. The anomalous course of Wollombi Brook can be best explained as being due to the upwarping of the relatively high tableland block, known as the Broken Back Range, during the Kosciusko Uplift. This relatively high block lies immediately to the north of the western-flowing part of the Wollombi Brook, and its uplift must have blocked drainage towards the north; it has a definite south-westerly tilt on its south-western side and these features caused the drainage to be diverted first to the west and finally to the north-north-west. The south-westerly direction of flow of the Upper Hunter River can be explained as being due to the piling up of the great thickness (nearly 2000 feet) of basaltic lava flows on the eastern (seaward) side of the watershed of that stream during the Upper Tertiary Period, and the subsequent uplift of the Barrington Tableland to a higher level than the Upper Hunter Tableland has again in the present cycle blocked drainage to the east and south-east.

The River Terraces.

Within the valley of the Hunter River, but particularly along the wide mature valleys of the Kingdon Ponds Creek and the Lower Hunter, there are, as was pointed out by the writer in 1923, several well-marked terraces or benches as follows:

(*a*) The Charleston Bench, 400 to 450 feet above present river level;
(*b*) The East Maitland Bench, 125 to 130 feet above present river level;
(*c*) The Raymond Terrace Bench, 15 to 20 feet above present river level.

(*a*) *The Charleston Bench* is particularly well developed in the coastal area immediately to the south and south-west of the town of Newcastle where it has a present elevation of 400 to 450 feet above sea-level; it also extends southward beyond the Hunter River watershed to at least as far south as Gosford. The village of Charleston lies on the surface of this bench and therefore affords a suitable name for it. This same bench is found to occur as far up the Hunter Valley as the town of Muswellbrook, where it is well developed to the south and east of that town, and has a present elevation there of about 900 feet, that is, about 430 feet above the level of the channel of the Hunter River at that locality. In this district it has been developed in strongly folded Permian strata and consequently is not due to local benching in weak horizontal strata, but has been produced by river erosion when the river flowed at the same level as the bench. This bench has been much dissected since it was uplifted to its present position, and has been largely removed.

(*b*) *The East Maitland Bench.*—This erosion level is very widely developed along the valley of the Hunter River from the coast to Muswellbrook and thence northward along the valley of Kingdon Ponds Creek to Wingen; as it is particularly well developed about the town of East Maitland, this affords a suitable name for it. It has a general elevation of about 125 feet above present river-level and is a definite rock bench cut alike in nearly horizontal strata and in folded strata, and is covered in places with a thin layer of river sands and gravels. In many places it extends almost to the foot of the existing valley sides, showing that there has been only limited valley widening since it was formed; since its uplift it has suffered considerable dissection, with the development of fairly extensive flood plains below it at present river levels, but the fact that it still survives over very

extensive areas, in many of which the strata out of which it has been cut consist of very weak shales, indicates that it is geologically young.

(*c*) *The Raymond Terrace Bench.*—This is an alluvial bench some 15 to 20 feet above sea-level and limited in its occurrence to the lower part of the Hunter River Valley, extending from West Maitland to the coast; at Largs near West Maitland a raised beach containing marine shells is associated with this bench; these features have been described by David (1907).

The Faulting and Warping.

Evidence for the existence of a number of tectonic scarps in this region has been given. Some of these scarps are probably fault scarps; some are due to monoclinal folding and some possibly to a combination of warping and faulting. These faults and folds fall into two definite groups, (*a*) those having a meridional or approximately north-south trend, that is, parallel to the north-south axes of uplift of the main tableland belt, and (*b*) those striking east-west, that is, transverse to (*a*); the more important of these are as follows:

(*a*) *Meridional faults and monoclines.*

1. The Woolomin Fault—western margin of Barrington Tableland.
2. The Wingen Fault—western margin of Upper Hunter Tableland.
3. The Cassilis Monocline—western margin of Goulburn River Tableland.

(*b*) *Transverse Faults and Monoclines.*

1. The Barrington Faults—southern margin of Barrington Tableland.
2. The Murrurundi Faults—southern margin of New England Tableland.
3. The Liverpool Range Fault (? monocline)—northern margin of Liverpool Ranges.
4. The Gulf Fault or Monocline—southern margin of Goulburn River Tableland.

As some of these have definitely faulted and displaced the Tertiary basalts they are obviously post-basaltic in age and all of them are considered to have been produced during the differential uplift which originated the existing tablelands (Kosciusko Uplift).

It is interesting to note that the Tertiary basalts attain their greatest thickness along some of these tectonic lines; adjacent to the Barrington-Woolomin faults, for example, these basalts range up to 2000 feet in thickness, and along the line of the Liverpool Range Fault (or monocline) they range up to 1500 feet in thickness; elsewhere they are much thinner. Also associated with the Gulf line of faulting or folding occur the large alkaline intrusions referred to by the writer (1932) in a previous paper; such lines therefore appear to have already been lines of weakness in the earth's crust before the present tablelands were uplifted.

It has already been pointed out that the relatively low tableland area drained by the Hunter River lies between two relatively higher tableland blocks, the Northern or New England Tableland on its northern side, and the Central Tableland on its southern side, and it is interesting to note that here the Central Tableland is definitely "stepped back" westward in relation to the Northern Tableland. Each of these two extensive tableland regions is divisible broadly into three belts parallel to one another, and with an approximately north-south trend, that is, parallel to the Main Divide and to the coast; in each case there is a relatively high central belt, which we may call belt B, 3000 feet and upward in altitude, flanked to the east and west by relatively lower belts, which we may call A and C respectively, whose general altitude varies from 1000 to 2000 feet

(even less in places). The coastal belt A of the Northern Tableland ends abruptly at its southern end at the ocean; reference to the map (Plate x) shows a marked westerly bend of the coast here, known as the Newcastle Bight, while belts B and C of the Northern Tableland at their southern end come opposite to belts A and B of the Central Tableland. This stepping back of the Central Tableland appears to be definitely associated with the transverse faults and flexures of the Hunter River area, and still further supports the view that the Cassilis geocol, as Taylor called this region, is a tectonic feature and not an erosional feature.

Summary and Conclusions.

In the descriptions already given it has been shown that the region drained by the Hunter River system was at one time a peneplain developed in strata ranging from Devonian to Jurassic in age; following a slight uplift of this peneplain, valleys were developed some 300 feet in depth. This valley development was interrupted by pronounced vulcanism, during which extensive lava flows were poured out over much of the area; these not only filled some of the valleys but poured over, in many places, the surface of the peneplain itself. Subsequent to the vulcanism, valley development continued until there had been produced an extensive series of very wide mature valleys, referred to in this paper as the "upland valleys". The whole region with its lava flows and upland valleys was then uplifted to form the existing tablelands ranging from 1400 to 5000 feet in altitude; this differential uplift was accompanied by extensive warping, monoclinal folding, and faulting. This has been followed by a compound cycle of erosion, which is still in progress, and the pre-existing streams, revived by the uplift, have dissected the tablelands to the early mature stage of development. In limited parts of the area, particularly in the far western portion about the headwaters of the Goulburn River, some of the uplifted Tertiary topography still survives and here the present-day streams may be seen heading back into the Tertiary "upland valleys".

These features are not peculiar to this region, but extend over the whole of the eastern part of the State, and their age and origin have already been discussed by the writer in a previous paper (1937); the events and the geological ages assigned to them were as follows:

1. Eocene to Miocene—a cycle of erosion during which the peneplain (Great East Australian Peneplain) was produced.

2. Epi-Miocene—an epeirogenic uplift which produced a series of low tablelands some 300 to 400 feet in altitude.

3. Lower Pliocene—erosion of valleys which in other parts of the State contain fossil leaves and fruits.

4. Lower Pliocene—widespread volcanic activity with the pouring out of floods of basaltic lavas.

5. Upper Pliocene—continuation of valley formation with the development of the "upland valleys".

6. Late Pliocene—the Kosciusko Uplift which produced the existing tablelands.

7. Pleistocene to Recent.—The existing cycle of erosion during which the tablelands have been dissected to their present condition. The erosion benches at 400 and 130 feet above present river level indicate pauses in the general uplift.

The evidence for the area now described fully confirms the above succession of events; under this scheme the Hunter River valley proper is post-Tertiary in age.

More recently H. G. Raggatt (1938) has suggested a Tertiary age for the Hunter River Valley, and it becomes necessary to examine the evidence put forward by him in support of this view. He has described the occurrence, at various places in the Hunter Valley lying between Singleton and Denman, of a layer of silicified sands and gravels ("grey-billy") lying upon an erosion surface some 130 feet above present river level, and he considers that the only way in which these deposits could have become silicified was by the pouring over them of basaltic lava flows; he admits, however, that no basalts occur on this level today. These supposed basalt flows are considered by him to have been of Tertiary age, and that therefore the Hunter Valley itself must be of Tertiary age.

The erosion level referred to is, of course, the one described in this paper as the East Maitland Bench; this bench is developed in many places in very weak strata; at East Maitland the strata are gently folded coal-measures consisting of interbedded shales and sandstones; at Denman and northward from there the strata are nearly horizontal shales, a very weak structure. Following an uplift of this bench (or possibly a corresponding lowering of sea-level) the Hunter River has today cut its channel down to present base-level, and has produced at this lower level a flood-plain of only moderate width and extent as compared with the original area of the bench itself, while the surviving parts of the latter have suffered only moderate dissection. These features all suggest that this bench is geologically young; had it originated back in the Tertiary Period it would surely have been largely removed by now, and had it ever been covered by basalt flows it is difficult to imagine how these could have been completely stripped off and the underlying weak shales left behind.

It is quite true of course that "grey-billy" occurs under basalt flows in many parts of New South Wales, but similar rocks also occupy extensive areas of the surface in the western part of the State where no basalts occur; these are considered to have been silicified by underground water ascending under the influence of capillarity under the conditions of the dry climate which exists there. The climate of that part of the Hunter Valley referred to by Raggatt is not so dry as the western part of the State; nevertheless it has a relatively dry climate as compared with most localities in Eastern New South Wales. On the map (Plate x) there is a heavy black line which indicates the approximate position of the 25-inch isohyet, and it will be noticed that it makes a marked bend to the east in the Hunter Valley extending almost to Singleton. At Denman the average rainfall over a long period of years is only about 22 inches, but this does not give a true picture because in some years the rainfall has fallen as low as 11 inches; such drought conditions may continue for several successive years, and in such dry years the rain that does fall is largely confined to a short part of the year with long intervening rainless periods. There is evidence from other parts of the world of epochs of much drier conditions during the Pleistocene Period than those which exist at present, and it is quite possible that such epochs of drier climate affected this part of the world also; one might even quote the deposits of "grey-billy" as evidence in favour of this view. Quite apart from these suppositions, however, there is the important fact that silicification of gravels is actually taking place in Eastern Australia today under the present climatic conditions. Dr. E. O. Marks has informed the writer that it is taking place in many places in Eastern Queensland, while the writer has recently observed in the Portland District of New South Wales deposits of silicified gravels in quite youthful gullies on the steep hillsides of that region. It appears

to the writer therefore that the silicified gravels described by Raggatt are not necessarily proof of the former existence of basalt flows immediately above them. Even if his conclusion is the correct one, it does not follow that such basalt flows are of Tertiary age as he suggests; in support of his view he quotes a statement by Dulhunty (1938) that Tertiary Basalts have flowed into the Goulburn Valley. Of the three localities mentioned by this writer one occurs in the Goulburn Valley at Crowie and a second in the valley of Wollar Creek near Wollar, and in both of these cases the details given of the altitude at which they occur show that the basalts flowed into the pre-Kosciusko "upland valleys" and not into the post-Kosciusko valleys of these streams. The third occurrence mentioned by Dulhunty is in the Bylong Valley near the junction of this stream with the Goulburn River; this occurrence has been visited by the writer and in his opinion it is not part of a lava flow, but is a large volcanic neck; in all of its features it closely resembles the undoubted basaltic volcanic neck which occurs near the head of the Bylong Valley at a place called The Gulf, and which was described by J. E. Carne (1903); a similar large volcanic neck also occurs a short distance east of the Main Divide on the Mudgee-Wollar Road. In many places in the region now being described Tertiary basalt flows cap the tablelands right on the edge of the present-day valley walls, upwards of 1000 feet in thickness in some localities, but in no cases known to the writer have such basalts flowed into the present-day valleys of the Hunter River or its tributaries. If the basalt flows postulated by Raggatt ever did exist, they would undoubtedly have been of Pleistocene and not of Tertiary age.

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EXPLANATION OF PLATE X.

Map of the Hunter River Watershed.

TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XVI–XVII.

By Consett Davis, M.Sc., Lecturer in Biology, New England University College.

(One hundred and eighteen Text-figures.)

[Read 31st July, 1940.]

XVI. THE GENUS *EMBIA* LATREILLE.

(Seventy-seven Text-figures.)

Genus Embia Latreille 1829.

Le Règne animal distribué d'après son organisation, par M. le Baron Cuvier, Nouvelle Édition, revue et augmentée; p. 257 (foot-note). No specific name given. Genotype, *Embia savignyi* Westwood, 1837, *Trans. Linn. Soc. London*, 17, p. 372.

Savigny (1809–1813) figured (Pl. ii, figs. 9–10) a species of the Order from Egypt, but no name was applied. Latreille (1825, p. 437) used the name Embie, as vernacular, and without description or reference to a previous description or figure; this use has therefore no taxonomic standing. Audouin (1827) used Embie with reference to Savigny's figure, but the name is still vernacular, and no standing can be attributed. In the same year Berthold made use of the form Embium, the first Latinized form; this, however, receives no consideration, being a nomen nudum.

Latreille (1829, p. 257), under the name *Embia*, gives a short description, together with a note that the insect to which he refers was figured by Savigny. Although *Embia* is here used alone, that is, as a uninomial, the genus dates from this record (cf. Opinions rendered by the International Commission on Zoological Nomenclature, Opinion 54, wherein certain genera of Rafinesque 1820, an author who was accustomed to use binary nomenclature, are confirmed as dating from 1820, though used by Rafinesque uninomially, without designation of species).

In 1832, Griffith and Pidgeon (ex Gray manuscript) described a Neotropical Embiopteron, *Olyntha brasiliensis*, *Olyntha* being designated a subgenus of *Embia* Latr. The plate illustrating this species, drawn by Westwood, was issued as by Griffith and Pidgeon in 1831, with the title 'Embius? Brasiliensis G. R. Gray'; the query applying, not to the identity of the species (as only one specimen was then known; see Westwood, 1837, p. 369), but apparently to doubt, at the time the plate was prepared, of the Latin ending to apply to the vernacular 'Embie' of Latreille (1825) and Audouin (1827). The generic name *Embius*, dating from 1831 (but corrected by its authors to *Embia* in 1832), is a homonym of *Embia* Latreille 1829, by application of Opinion 115 of the International Commission. The name *Olyntha* is also invalidated by *Olynthus* Hübner 1818 (Coleoptera), a member of the same Class. The Neotropical series is not congeneric with the North African series (*Embia* Latreille), and a new name is required to replace the invalidated *Olyntha*.

In 1837 Westwood described *Embia savignyi*, his description being based, not on any actual specimen, but on Savigny's figure, the original of which is the type of the species. As Savigny's figure lacks certain essential details (e.g. of the

terminalia), and as there has been some lack of agreement on the limits of the species, a neotype from the Egyptian region is described below in order to fix the species permanently.

It would be misleading to accept *brasiliensis* Griffith and Pidgeon 1831 as the genotype (by monotypy) of *Embius* (*Embia* homonym), and this course is rendered unnecessary by the query on the plate (1831) of these authors. *Embia savignyi* Westwood 1837 may be accepted as genotype of *Embia* Latreille 1829; this is indeed the current procedure (cf. Krauss, 1911; Enderlein, 1912). The Neotropical series, of which *Olyntha brasiliensis* is a typical example, will receive a name to replace the invalidated *Olyntha*, and an adequate generic description, in the subsequent part of this series; Griffith and Pidgeon's criteria for its separation (subgenerically) from *Embia* are less important than other criteria which might have been chosen from the specimen named by these authors. This series is confined to the New World, just as *Embia* Latreille is confined to the Old World (Mediterranean Region south to South Africa).

The genus *Embia* may be defined as follows, the concept being formed on agreement with the genotype in characters considered sufficient for generic differentiation, but not so embracing as those used previously (e.g. Enderlein 1912), which give too wide limits to the genus, and assemble in it unrelated forms:

Old-World Embioptera, the males with the following characters: Winged or wingless; if winged, veins well developed, R_1 usually confluent subterminally with R_{2+3}, R_{4+5} forked, M simple except for individual anomalies; anterior branch of cubitus simple, occasionally with additional pigment-bands between it and the cubital stem, but these are not usually accompanied by veins. Hind tarsi with one terminal bladder on the ventral side of the first segment, the rest of the plantar surface of the metatarsus carrying strong setae. Terminalia with tenth abdominal tergite completely cleft longitudinally; right hemitergite massive, with a posteroventral process, usually acute, and an inner subelliptical flap of chitin connected posteriorly, anteriorly separated by membrane. Process of left hemitergite simple, tapered. First segment of left cercus clavate (usually not excessively so), echinulate internally. Other segments of cerci subcylindrical. Right cercus-basipodite small, subannular; left cercus-basipodite with a process. Hypandrium produced backward to an obtuse process to the right of the mid-line.

The characters differentiating each related genus, dealt with previously in this series, from *Embia* in the present sense, have been included under those genera; the differentiation of the Neotropical series usually referred to *Embia* will be shown in the subsequent part of this series.

The genus *Euembia* Verhoeff (1904) is an absolute synonym of *Embia*. The genus *Monotylota* Enderlein 1909 (*Zool. Anz.*, 35, p. 188; genotype *Embia ramburi* Rimsky-Korsakov 1905, ibid., 29, p. 434) must also be rejected as a synonym. As will be seen from the re-description of *E. ramburi* (infra), its terminalia agree in every respect with the generic description, as do its tarsi; it could not be separated generically on any character but the absence of wings in the male (present in *E. savignyi*; absent in *E. ramburi*). It is known that the absence of wings is a highly convergent character in the Embioptera, and it is in fact a character of very little taxonomic value; winged and wingless forms of a single species of some genera may occur in the same colony (cf. Davis, 1938, p. 254, and papers there cited). Winglessness, unsupported by any other character, cannot be regarded as a generic criterion in this Order. Species with winged males also hybridize with species with wingless males, according to Friederichs (1934).

EMBIA SAVIGNYI Westwood 1837. Figs. 1–16.

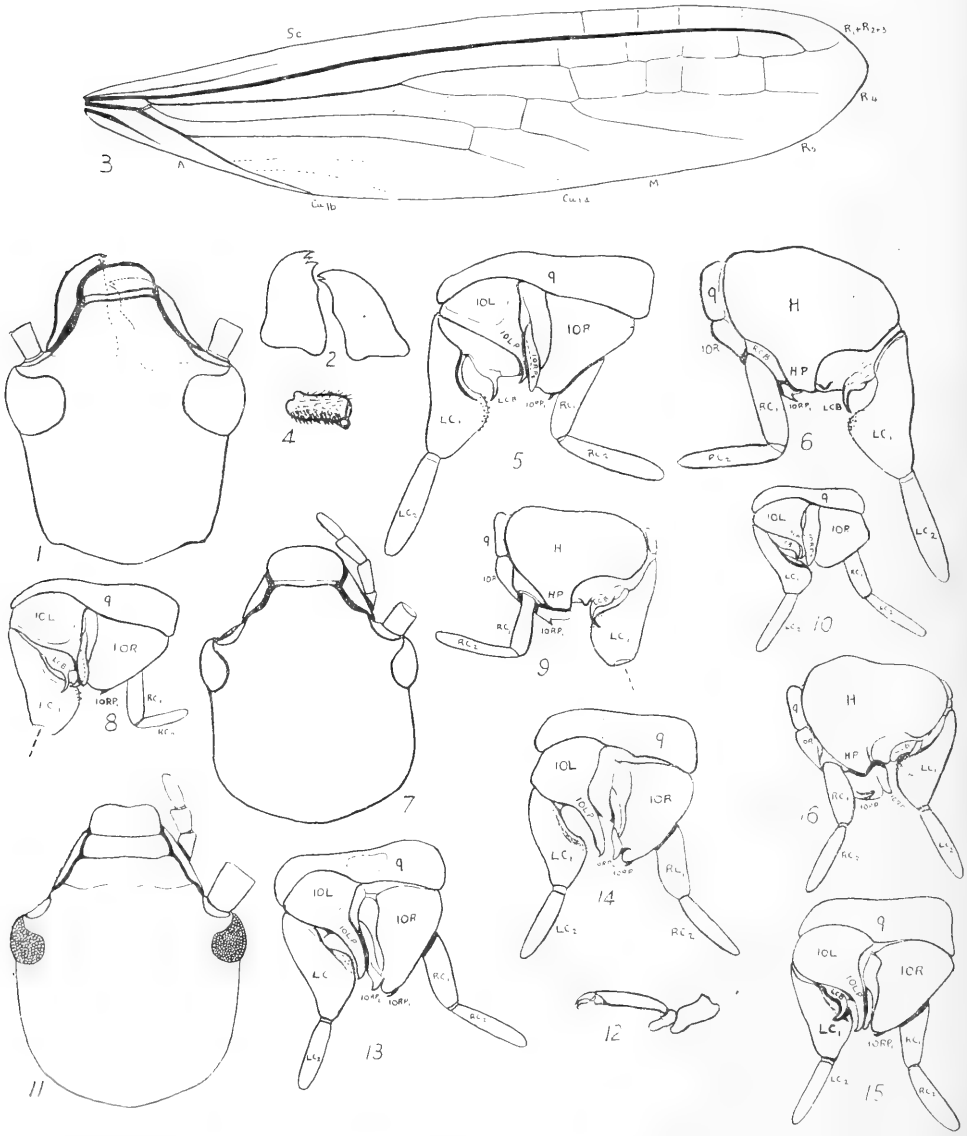
Trans. Linn. Soc. London, xvii, p. 372.

The lack of any specimen serving as a type, as noted above, has led to some variation in different authors' concepts of the species. To obviate this, a male has been selected, labelled as neotype, and deposited in the British Museum of Natural History. It agrees with the specific concept of Krauss (1911) and Werner (1912), but differs in some respects from the specimen figured under this name by Enderlein (1912, fig. 12). This specimen (Berlin Museum) has the left cercus-basipodite (ast_9 of Enderlein's figure) different from the neotype here named. Enderlein did not name his specimen neotype, nor did he in any way indicate that it was in future to represent the species; it would be unwise to select it as neotype at the present juncture, as, to judge from Enderlein's figure, some structures (particularly the left cercus) have been distorted, apparently by over-maceration and too liberal application of pressure to the cover-slip. It appears to be specifically distinct from the neotype, but in view of its distortion, and the lack of detailed locality, it cannot be named.

♂ (neotype). Length 13 mm.; head 2·0 mm. × 1·6 mm.; forewing 10·8 mm. × 2·4 mm.; hindwing 10 mm. × 2·4 mm. General colour (dry) pale ferruginous brown, terminalia darker brown, eyes black; wing-veins dark brown, bordered by bands of pale ferruginous brown. Head (Fig. 1) with eyes large, rather prominent, sides behind eyes converging slightly; posterior margin with a slight concavity on each side, just within the angle with the lateral margin. Antennae incomplete (according to Krauss, l.c., 19-segmented). Mandibles (Fig. 2) with incurved acute teeth terminally and subterminally, the left with three, the right with two. Wings (Fig. 3) with R_1 confluent subterminally with R_{2+3}; R_{4+5} forked, fork subequal to stem in length; media simple in all wings, distinct except at distal extremity; main stem of cubitus (Cu_{1b}) with a long, well-developed anterior branch (Cu_{1a}); between this and the stem there is an additional pigment-band (two in the right forewing; represented by dotted lines in Fig. 3), not supported by any indication of a vein. Anal distinct, rather long. Cross-veins moderately frequent.

First tarsal segment of hind legs (Fig. 4) with only the terminal ventral bladder present; remainder of ventral surface clothed evenly with strong setae. Terminalia (Figs. 5–6) with tenth abdominal tergite completely divided longitudinally; right hemitergite (10R) massive, subtriangular, with a postero-ventral process ($10RP_1$), short and acute, directed slightly to the left. Inner margin of 10R carrying a flat subelliptical chitinous flap ($10RP_2$), separated from 10R by membrane except at its posterior limit. Left hemitergite (10L) smaller than 10R, subtriangular, inner margin produced backward to a thin process (10LP), curved to the left, acute. Right cercus with two subcylindrical segments (RC_1, RC_2), arising from a small subannular cercus-basipodite (RCB). First segment of left cercus (LC_1) with inner margin smoothly dilated in an echinulate lobe in the distal third; concavity of inner margin basad to lobe weakly channelled by a shallow longitudinal furrow. Second segment (LC_2) subcylindrical. Hypandrium (H) produced back to an obtuse process (HP) somewhat to the right of the mid-line. Left cercus-basipodite (LCB), placed between HP and base of LC_1, produced backward to a rather slender, acute process, curving outward.

Locality.—The labels on the neotype (British Museum) are: 'G. R. F. Medani, H. W. Bedford, 22.12.22. Sudan Govt.'; 'Blue Nile. A125'; 'Embia savignyi, det. Friederichs 1936'.



*Figs. 1-6.—*Embia savignyi* Westw., neotype ♂. 1. Head from above, × 20. 2. Mandibles from above, × 20. 3. Right forewing, × 10. 4. First segment of hind tarsus viewed laterally, × 20. 5. Terminalia from above, × 20. 6. Terminalia from below, × 20.

Figs. 7-9.—*Embia savignyi* Westw., variant ♂ from Blue Nile region. 7. Head from above, × 20. 8. Terminalia from above, × 20. 9. Terminalia from below, × 20.

Fig. 10.—*Embia savignyi* Westw., ♂ (type of *E. enderleini* Esb.-Petersen). Terminalia from above (magnification not stated. After Esben-Petersen, 1915, fig. 11).

Figs. 11-16.—*Embia savignyi* Westw., ♂ (type of *Embia socia* Navás). 11. Head from above, × 20. 12. Hind tarsus viewed laterally, × 20. 13-15. Terminalia from above, varying aspects, × 20. 16. Terminalia from below, × 20.

Note.—The neotype agrees with Savigny's figure, as far as it goes, although Savigny's specimen had a venational anomaly in the right forewing (R_4 forked). It shows the anterior branch of the cubitus (Cu_{1a}) very long, as in the neotype, but the accessory pigment-bands of the neotype are not indicated in Savigny's figure; their presence is, at all events, an individual character (cf. also Enderlein, 1912, fig. 13, forewing), and they are absent in many specimens from the Egyptian region correctly referable to *E. savignyi*.

The exact structure of the specimen studied by Savigny can never be determined, and the neotype, selected arbitrarily, must stand for the species in future.

Variation and synonymy.—A second specimen from the Blue Nile region (coll. E. S. Crespin; British Museum) must be considered conspecific with the neotype, but shows some interesting variations. The head (Fig. 7) has smaller eyes, and the sides behind the eyes diverge slightly at first; the posterior margin is more smoothly rounded (in the characters of the head, this specimen agrees with *E. mauritanica* Lucas, q.v.). The general colour is a little darker than in the neotype, and the dimensions less (length 9 mm.; head 1·8 mm. × 1·4 mm.; forewing 7 mm. × 1·7 mm.; hindwing 6 mm. × 1·7 mm.). The cubitus has an additional pigment-band (between Cu_{1a} and the stem) only in the left forewing. The terminalia (Figs. 8–9) are scarcely distinguishable from the neotype.

For further references to the variability in colour and size, and to the distribution, the works of Krauss (1911), Werner (1912) and Karny (1923) should be consulted; all, however, may have a somewhat wider concept of the species than the present.

The following species seem to be synonyms with *E. savignyi*:

Embia aegyptiaca Blanchard, 1845, *Hist. nat. des Insectes*, 3, p. 47 (Paris).

Embia enderleini Esben-Petersen, 1915, *Ent. Mitt.*, iv, nos. 1–3, p. 86, figs. 10–11.—As Karny (1923) has already noted, there seems little reason for the separation of this species. It is therefore provisionally rejected as synonymous. The location of the type is not stated. Esben-Petersen's description may be summarized as follows: ♂. Colour as in the neotype of *E. savignyi*; antennae with 24 segments; wings as in the neotype, but without additional pigment-bands in the cubital system; terminalia (Fig. 10, after Esben-Petersen) indistinguishable from the neotype, except that the inner face of the first segment of the left cercus has a more marked longitudinal concavity basad to the echinulate lobe. Length 10·5 mm., of forewing 7·5 mm., of hindwing 6·5 mm.

Locality.—Dabba el Gardega, White Nile, 7/3/13.

Embia socia Navás, 1929, *Rev. Zool. Bot. africaines*, 18, fasc. 1, p. 108, fig. 19.—The following re-description of the unique type ♂ (Mus. Congo, Tervueren) should suffice to prove the synonymy with *E. savignyi*: Length 9·5 mm., of forewing 6 mm.; head (Fig. 11) 2·0 mm. × 1·6 mm., form more as in figure 7 than in neotype; antennae 3·2 mm., with 22 segments. Wings as in the type of *E. enderleini*; hind tarsi (Fig. 12) as in the neotype. Terminalia (Figs. 13–16) as in the neotype. *Locality*: Radjaf, Soudan, 30.v.1927, L. Burgeon. The colour (rather dark brown)

* All setae omitted except in Figs. 4, 25, 50 and 72. Original figures all based on camera lucida outlines except Figs. 17-23, 29-31, 35-38, 45-52, and 70-74, which were prepared with the constant use of an ocular micrometer. Conventional lettering for venation.

9, ninth abdominal tergite; 10L. 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, $10RP_2$, posterior and inner processes of 10R; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; H, hypandrium; HP, process of H.

and head structure agree with the second specimen discussed above, but this cannot be allowed as distinct from *E. savignyi*.

Donaconethis ehrenbergi Enderlein, 1909, *Zool. Anz.*, 35, p. 178.—The occasional forking of the media in one or more wings has been noted for *E. savignyi* by Krauss (1911, p. 64, and Pl. v, fig. 21D). This probably explains the identity of *Donaconethis ehrenbergi* End.; if Enderlein's figure of the terminalia (1912, fig. 70) actually refers to his type (as he suggests), then there can be no doubt as to the synonymy. The terminalia, according to this figure, have no resemblance to the genus *Donaconethis*, but agree exactly (allowing for distortion) with the neotype of *E. savignyi* Westw.

EMBIA MAURITANICA Lucas, 1849. Figs. 17–23.

Exploration scientifique d'Algérie, Zoologie, 3, p. 111, Pl. 3, figs. 2a-n.

Lucas's types (Mus. Paris) are in an excellent state of preservation (in alcohol), and include five males. The locality is given merely as 'Algérie'; the detailed locality of the type series is unknown, but probably is Central or Eastern Algeria. The re-descriptions of the species by Krauss (1911) and Enderlein (1912) were not based on type material. The following details refer to the type series:

♂. Length 8·5–15 mm. (8·5, 10, 10·5, 13, and 15 mm. for members of the type series). Length of forewing 6–10 mm.; head 2·0–2·3 mm. × 1·5–1·8 mm. General colour (in alcohol) golden-brown, head darker, eyes black; anterior abdominal sclerites paler brown; wing-veins dark brown, bordered by smoky-brown bands, inter-venal lines hyaline. Head (Fig. 17) with eyes small, sides behind eyes diverging at first, rounded behind. Mandibles (Fig. 18) as in *E. savignyi*; wings as in *E. savignyi*, the cubitus two-branched, without additional pigment-bands. Hind tarsi as in *E. savignyi*. Terminalia (Figs. 19–23) very similar to *E. savignyi*, the left hemitergite (10L) with its outer margin slightly elbowed at the origin of the process (10LP), the first segment of the left cercus (LC_1) a little thicker, the internal swelling more distal in position, and the process of the left cercus-basipodite (LCB) shorter, and arising from nearer to the hypandrium (H).

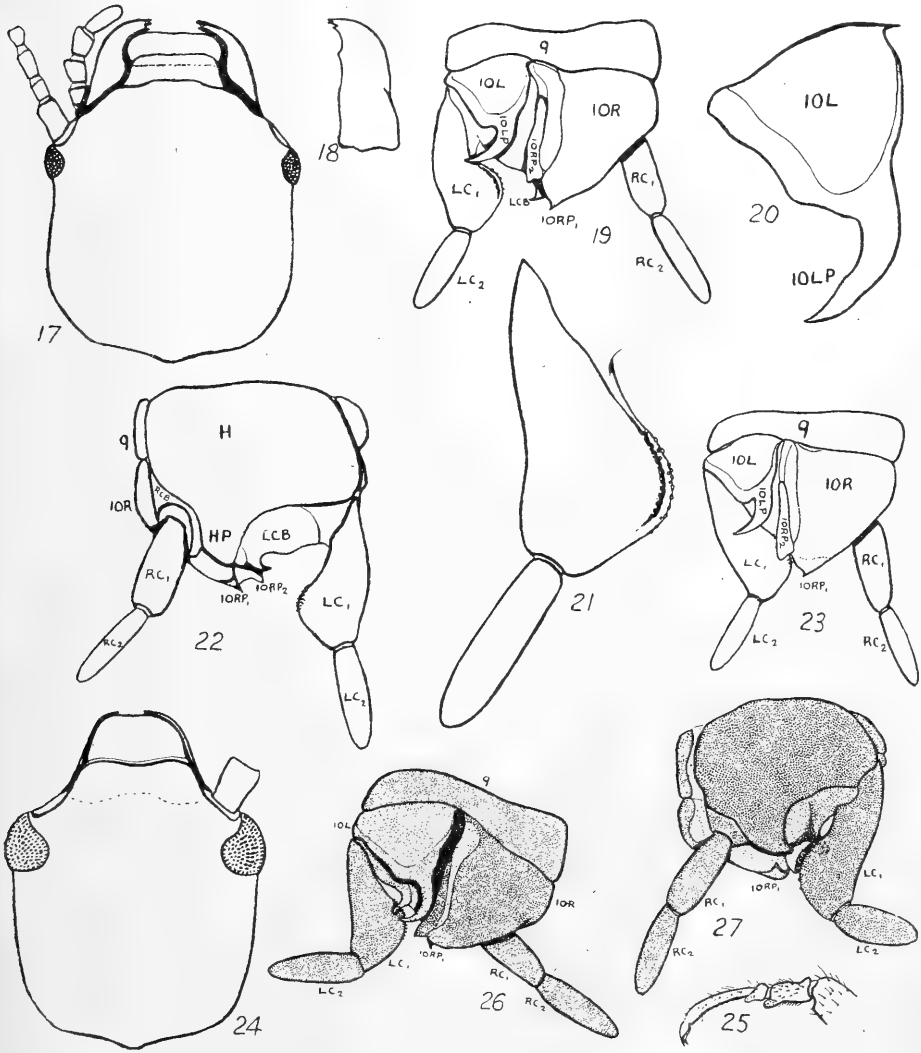
♀. Length 11–12 mm.; general colour mid-brown to rather dark brown; tarsi as in the male. As is usual in this Order, there is little to distinguish the female from other species of the genus, or even of some unrelated genera.

Note.—The localities cited by Krauss (1911) (Spain, West and South Algeria, Canary Islands, Syria, and British East Africa) should be viewed with distrust; many of the records are based on larvae, and even where males were seen by Krauss (Cartagena, Spain; Ain Sefra, Western Algeria; Biskra and Ghardeja, Southern Algeria; Teng-Tina, Syria; and British East Africa), the identification was probably based on dried, unprepared material, and the specific limits may be assumed to have been broader than the present concept, based on the type series. The record for British East Africa represents the type of *E. verhoeffi* Fried. (q.v.), an entirely different species. The locality is actually Portuguese East Africa (fide Enderlein, 1912, p. 44).

The only specimen, other than the type series, seen by me, that I would unhesitatingly refer to *E. mauritanica*, is from Biskra, Algeria (♂; British Museum; coll. G. C. Champion); several other series are discussed below, in each case being somewhat atypical.

Variation.—A male from Kébili, Tunisia (Mus. Comparative Zoology, Harvard University) may be referred to *E. mauritanica*, though it shows some affinities with other species. The dimensions are: Length 11 mm.; head 2·2 mm. × 1·7 mm.; forewing 8 mm. × 2 mm. General colour (dry) dark brown. Head (Fig. 24) with

eyes larger, and sides more convergent, than in the types, in this respect varying towards the neotype of *E. savignyi*. Tarsi (Fig. 25) as in the types, and throughout the genus. Terminalia (Figs. 26–27) as in *E. mauritanica*, types, but with the first segment of the left cercus and the left cercus-basipodite tending towards



Figs. 17-23.—*Embia mauritanica* Lucas, ♂ (type series). 17. Head from above, × 19. 18. Left mandible from below, × 19. 19. Terminalia from above, × 19. 20. Left hemitergite of tenth abdominal segment, from above, × 25. 21. Left cercus, different aspect from fig. 19, × 35. 22. Terminalia from below, × 19. 23. Another specimen from the type series: terminalia from above, × 19.

Figs. 24-27.—*Embia mauritanica* Lucas, var., ♂ from Kébili, Tunisia. 24. Head from above, × 20. 25. Hind tarsus viewed laterally, × 20. 26. Terminalia from above, × 20. 27. Terminalia from below, × 20. (Stippling on figs. 26-27 to indicate degree of pigmentation and sclerotization.)

E. savignyi Westw. (supra) and *E. tunetana* Nav. (infra). The terminalia seem to agree with Enderlein's figure of *E. savignyi* (1912, fig. 12), which is not typical of that species in the present sense.

A male in the British Museum (Azazga, Kabylie, Algeria, G. C. Champion) varies less from the type series of *E. mauritanica* than does the above.

Other series are considered under *E. tunetana* Nav.

EMBIA FIBULATORIA Enderlein 1912. Fig. 28.

Coll. zool. de Selys-Longchamps, fasc. 3, p. 111, fig. 73.

♂ (after Enderlein, l.c.). Length 8·5–10 mm.; head 1·7–2·0 mm. × 1·2–1·4 mm.; forewing 7·5–8·5 mm. × 1·7–2·1 mm.; hindwing 6·8–7·8 mm. × 1·7–2·1 mm. General colour pale yellowish-brown, eyes and antennae darker, wings with dark-brown veins bordered by pale-brown bands. Description of head outline agrees with that of *E. savignyi*. Terminalia (Fig. 28, after Enderlein) as in *E. savignyi*, but both the process of the left hemitergite (10LP) and the left cercus-basipodite (LCB) longer and thinner. Enderlein's figure omits the structures appended to the right hemitergite, which may be assumed to agree with *E. savignyi*.

♀ unknown.

Locality.—Inner Cameroons (Rei Buba, Djurum, Garena, Ubao, and Tschad-See (Lake Chad)); types in Berlin and Stettin Museums.

This species is clearly differentiated from the typical *E. savignyi*, on the form of the left hemitergite and basipodite, but the difference may prove to be only racial (subspecific).

EMBIA TUNETANA Navás 1919. Figs. 29–31.

Mem. Pont. Accad. Romana dei Nuovi Lincei, Series ii, 5, p. 26.

Navás (l.c.) states that the type (♂), from Tunisia (coll. E. Le Moult) is in his own collection. In the Paris Museum is a male labelled: 'Embia tunetana Nav.; Navás S.J. det.'; 'Tunisie. E. Le Moult'; 'Typus' (Navás's pink manuscript type label). I assume this to be the type, transferred at some time from Návas's own collection. It serves as the basis of the following description:

♂. Length 10 mm.; head 2·0 mm. × 1·7 mm.; forewing 7 mm. × 1·9 mm.; hindwing 6 mm. × 1·8 mm. General colour (dry) dark brown, anterior part of head reddish-brown, eyes black; wing-veins dark brown, bands smoky-brown, inter-venal lines hyaline. Head (Fig. 29) as in *E. mauritanica* Lucas. Terminalia (Figs.

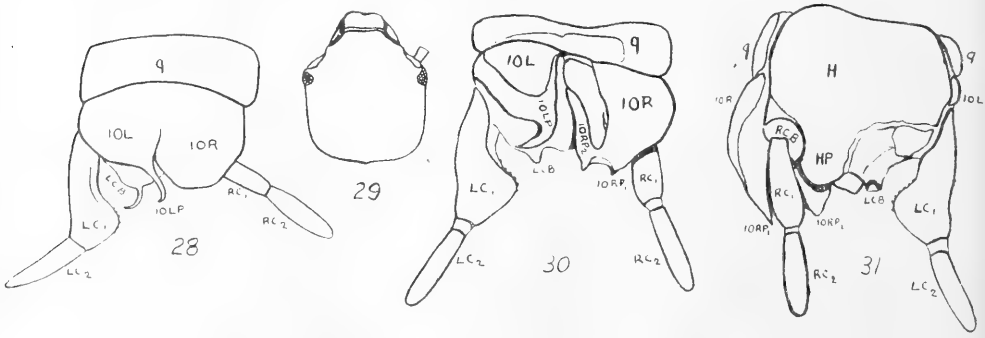


Fig. 28.—*Embia fibulatoria* Enderlein, type ♂ (after Enderlein, 1912, fig. 73). Terminalia from above. × 27.

Figs. 29–31.—*Embia tunetana* Navás, holotype ♂. 29. Head from above, × 10. 30. Terminalia from above, × 19. 31. Terminalia from below, × 19.

30–31) distinguishable from *E. mauritanica* only in the left cercus-basipodite (LCB), which is terminally obtuse, basally directed upwards, then curved downwards.

♀ unknown.

The left cercus-basipodite may be an individual character, possibly even teratological. The study of further Tunisian specimens may indicate, however, that it is a constant character for that region, in which case the status would still probably require reduction (to a geographic race of *E. mauritanica*). Preliminary data on this problem are to be found in three males in the British Museum ('Hammam-Meskoutine, May 13–17, 1914, W.R. and K.J.'), which agree closely with the type of *E. tunetana*, the left cercus-basipodite being perhaps a little longer and more slender, but bent up, and terminally down-curved and obtuse, as in the type. A male in the British Museum (Tozeur, S. Tunisia, G. C. Champion, 1913) agrees with the above series in most characters, but has the head rather more as in *E. savignyi* (neotype), the sides behind the eyes being straighter and more convergent than in the typical form common to *E. mauritanica* and *E. tunetana*.

EMBIA RAMBURI Rimsky-Korsakov 1905. Figs. 32–34.

Zool. Anz., 29, p. 434 (larva).—*Monotylota ramburi* (R.-Kors.), Enderlein, 1909, l.c., p. 188; 1912, l.c., p. 65.

Rimsky-Korsakov's description refers to a larva from Villefranche, French Riviera. Some knowledge of the structure of the males from this locality has been given by Friederichs (1906) and Krauss (1911, p. 57, Text-Figure C, from an unpublished figure by Friederichs; this figure is reproduced here, Fig. 32). It would be beneficial if a neotype (or allotype) male from the type locality could be collected, fully described, and lodged in some museum. The present specific concept has rather vague limits, due to the general classification as *E. ramburi* by some authors (e.g. Friederichs, 1934) of any wingless male with terminalia agreeing with the present generic concept of *Embia*, regardless of locality. Thus Friederichs (l.c.) refers *E. biroi* Krauss 1911 (infra) to '*Monotylota*' *ramburi*,

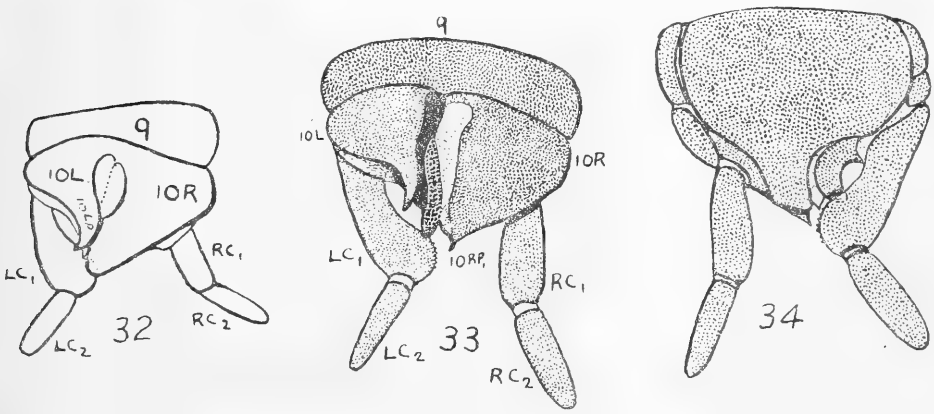


Fig. 32.—*Embia ramburi* R.-Kors., ♂ from Villefranche. Terminalia from above. Magnification not stated (after Krauss, 1911, Text-figure C, from an unpublished figure by Friederichs).

Figs. 33-34.—*Embia ramburi* Rimsky-Korsakov, ♂, Ronda, Spain (det. Rimsky-Korsakov). 33. Terminalia from above, × 40. 34. Terminalia from below, × 40. (Stippling as in figs. 26-27.)

and also identifies a male from Arabia, with different terminalia, as this species. Some wingless males, with terminalia on the general plan found in *Embia*, may be formae apterae of known winged species, and some species known only as wingless (*Monotylota* of Enderlein) may prove to possess winged forms. A general study of the Mediterranean species, from a geographic standpoint, and allowing for the unimportance of the presence or absence of wings, should give very interesting results.

I have seen no specimens from the type locality; the following description is from a male (Ronda, Spain, 2500 ft., 30.6.25, Sheppe) and female (Grazalama, Spain, 2500 ft., 29.6.25, in cork-oak woods), both determined as *E. ramburi* by Rimsky-Korsakov himself. These specimens are in the Museum of Comparative Zoology, Harvard University. The male terminalia agree sufficiently closely with descriptions of specimens from Villefranche (Friederichs, 1906, and 1923, fig. 3; Krauss, 1911, l.c.; cf. Figs. 32 and 33).

♂. Length 9 mm.; wingless. General colour very dark brown. Head rather narrow, eyes small. Hind tarsi as throughout the genus. Terminalia (Figs. 33–34) with right hemitergite as in *E. savignyi*; process of left hemitergite (10LP) much broader, and less curved, than in *E. savignyi*. First segment of left cercus (LC_1) slightly and smoothly dilated inwards distally, inner face of dilation echinulate. Left cercus-basipodite (LCB) a small plate curved outward to a subobtuse end. Other characters as in *E. savignyi*.

♀. Larger and paler. Thoracic sclerites, legs, and first abdominal sternite as in the ♂.

Note.—The additional localities listed by Krauss (1911), Enderlein (1912) and Friederichs (1934) should be treated with some doubt, until a full review of the terminalia of males from the type locality and elsewhere can be made. Further details of the colour, etc., of both sexes from the type locality can be obtained from Friederichs (1906).

Species probably synonymous with *E. ramburi* have been discussed earlier (Davis, 1939, Pt. xii of this series). They are: *Haploembia laufferi* Navás, *H. duplex* Navás, *H. codinai* Navás, *Embia cephalotes* Navás, and *E. silvanoi* Navás.

Embia algerica (Navás 1930). Figs. 35–38.

Haploembia algerica Navás, 1930, *Brotéria*, Série Zoológica, xxvi, fasc. 3, p. 136, fig. 45.

The following description is from the type (Mus. Paris):

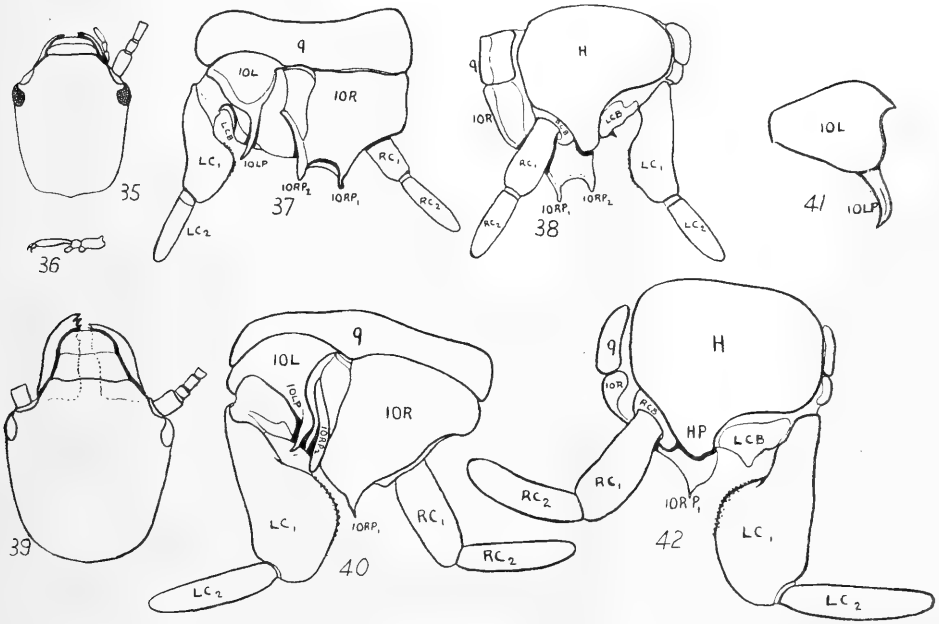
♂. Length 6·5 mm.; head 1·4 mm. × 1·0 mm.; wingless. General colour dull black, segments of legs and antennae dark brown. Head (Fig. 35) narrow, eyes small, placed far forward, sides behind eyes converging only slightly. Antennae with 14 segments (incomplete?). Hind tarsi (Fig. 36) with only one metatarsal bladder, as throughout the genus. Terminalia (Figs. 37–38) much as in *E. mauritanica*; posterior process of right hemitergite ($10RP_1$) obtuse, directed backward; space between $10RP_1$ and inner process ($10RP_2$) rather extensive, concave (this may be due merely to the configuration of the parts when studied, perhaps distorted by drying or preparation). Process of left hemitergite (10LP) long, acute, much thinner than in *E. ramburi* or *E. mauritanica*, only a little curved to the left; 10LP is in this respect rather similar to the winged species *E. fibulatoria* End., also West African. First segment to left cercus (LC_1) reminiscent of *E. savignyi* (neotype specimen). Left cercus-basipodite (LCB) with left-hand part folded upwards as a long obtuse flange, and with a small subobtuse

spine near the inner limit, i.e. near the process of the hypandrium. Other structures as in *E. savignyi* and *E. mauritanica*.

♀ unknown.

Locality.—Agadir, Morocco ('Miss. Lecerf and Talbot, Grand Atlas, 28.iv. à 9.vi.1927'). In the Paris Museum there is another male with the same locality label, but without Navás's determination or type label. It is superficially similar (size, colour, etc.); time did not permit a detailed study of the terminalia.

This species appears to be quite distinct on the form of the terminalia, and the dull black coloration is exceptional. It would be interesting to compare with it males from the Canary Islands, where the genus is reputed to occur.



Figs. 35-38.—*Embia algerica* (Navás), holotype ♂. 35. Head from above, × 15. 36. Hind tarsus viewed laterally, × 15. 37. Terminalia from above, × 28. 38. Terminalia from below, × 28.

Figs. 39-42.—*Embia silvestrii*, n. sp., holotype ♂. 39. Head from above, × 20. 40. Terminalia from above, × 40. 41. Left hemitergite from above and to the left, × 40. 42. Terminalia from below, × 40.

EMBIA SILVESTRII, n. sp. Figs. 39–42.

In the Paris Museum is an alcoholic male from Ouled Messelem, Algeria, determined by Silvestri as *Embia ramburi* R.-Kors. In view of the distinct structure of the terminalia, it is described as a new species.

♂. Length 7 mm.; head 1·6 mm. × 1·1 mm.; wingless. General colour dark brown, shiny, eyes black. Head (Fig. 39) similar to the preceding species; antennae with 21 segments on each side, length 2·8 mm. Hind tarsi with one ventral bladder distally on the first segment. Terminalia (Figs. 40–42) differing from *E. ramburi* in the process of the left hemitergite (10LP), narrower and somewhat contorted, curved outward, distally acute; the left cercus-basipodite

(LCB) obtuse, directed upward; and the first segment of the left cercus (LC_1) with distal two-thirds of inner face expanded in a large rounded echinulate lobe. Other characters as in *E. ramburi*, *E. savignyi*, etc.

♀ unknown.

Locality.—Ouled Messelem, Algeria, 25/5/1893 (holotype ♂ in Muséum d'Histoire naturelle, Paris). The left cercus immediately differentiates this from any other known species of *Embia*, winged or wingless.

EMBIA BIROI Krauss 1911. Figs. 43–44.

Zoologica, Hft. 60, Bd. 23, p. 59, Pl. iii, figs. 18–18D.—*Monotylota biroi* (Krauss), Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, p. 104.

♂ (after Krauss, l.c.). Length 13–15 mm.; length of head approximately 2·3 mm.; wingless. General colour reddish-brown to dark chestnut-brown, shiny. Head broadly elliptical, rounded behind; antennae with 23 segments. Terminalia (Figs. 43–44, after Krauss, l.c., Pl. iii, figs. 18A–B) much as in *E. mauritanica*, the first segment of the left cercus (LC_1) slightly different in form (dilation less distally placed), but possibly within the range of individual variation for *E. mauritanica*. Left cercus-basipodite (according to Krauss's figures) obtuse, but according to his verbal description produced to a narrow process, acute, terminally bent hook-wise, adjacent to the penis (recte process of hypandrium).

♀. See Krauss, l.c., p. 60. Not of taxonomic importance.

Locality.—Gafsa, Tunisia, 2 ♂, 1 ♀, coll. L. Biró (Mus. Budapest, types).

Friederichs (1934, p. 409) states with assurance that the species, of which he had examined the (dried) types, is synonymous with *E. ramburi* R.-Kors. I attribute more weight to Krauss's careful figures than to this statement. According to these figures, *E. biroi* differs from *E. ramburi* in the terminalia, the most important systematic criterion. It is possible, however, that it may prove to be a forma aptera of *E. mauritanica*, which occurs in the same region; this may be decided at a later date.

EMBIA GAILLARDI Navás 1922. Figs. 45–47.

Rev. Acad. Cienc. Zaragoza, vii, p. 28.

The following re-description is from the unique type (Mus. Paris):

♂. Length 10 mm.; forewing 7 mm. × 1·7 mm. General colour pale ferruginous, eyes black; wing-veins dark brown, bordered by mid-brown bands. Head, wings and tarsi as in *E. mauritanica* (in the right forewing, R_4 is branched terminally; Fig. 45). Terminalia (Figs. 46–47) very similar to *E. savignyi* and *E. mauritanica*; left hemitergite (10L) as in the latter species, left cercus basipodite (LCB) as in the former; first segment of left cercus (LC_1) more as in *E. mauritanica* than in *E. savignyi*, the internal lobe less smoothly rounded (Fig. 46), though apparently smooth from some aspects (Fig. 47).

♀ unknown.

Locality.—'Haut Dahomey: Marakou (Mission Tilho), Dr. R. Gaillard, 1910, Juillet.'

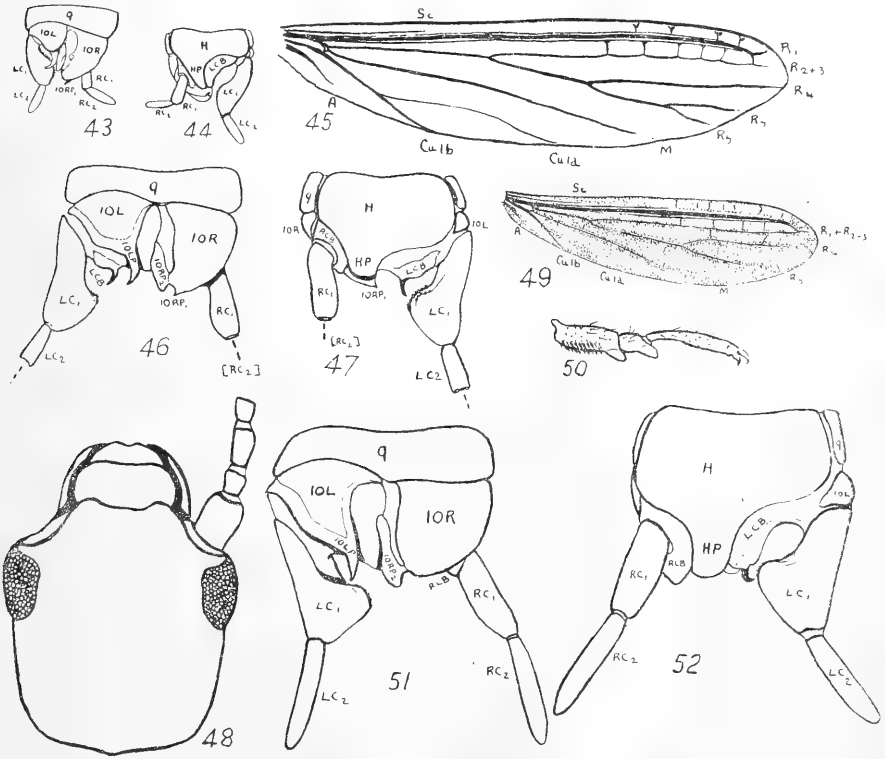
Whether this specimen is distinct from *E. mauritanica* and *E. savignyi* may well be doubted; perhaps all three, together with *E. fibulatoria* End. and some others, are races of the same species. The present course is to place on record the facts relating to the types and to leave it to future workers, assisted by further records, to weigh the taxonomic values, and the necessary status allowable to each name.

EMBIA CHUDEAUI Navás 1922. Figs. 48–52.

Embia (*Rhagadochir*) *chudeaui* Navás, 1922, *Rev. Acad. Cienc. Zaragoza*, vii, p. 29.

The following re-description is from the unique type (Mus. Paris):

♂. Length 6 mm.; forewing 6 mm. × 1·1 mm.; hindwing 4·3 mm. × 1·1 mm.; head 1·2 mm. × 0·9 mm. General colour pale yellowish-brown, eyes black; wings with R_1 golden-brown, other veins, and narrow bordering pigment-bands, very pale brown. Head (Fig. 48) rather narrow, eyes not prominent, sides behind eyes slightly converging, smoothly rounded behind. Wings (Fig. 49) normal for the genus, except that the veins, especially Cu_{1a}, are weaker than usual. Hind tarsi (Fig. 50) normal for the genus. Terminalia (Figs. 51–52) similar in general arrangement to *E. savignyi*, but with various differences in detail, warranting specific rank; process of left hemitergite (10LP) short, little curved; first segment of left cercus (LC_1) with inner margin, distad to apex of echinulate lobe, almost



Figs. 43-44.—*Embia biroi* Krauss, holotype ♂ (after Krauss, 1911, Pl. iii, figs. 18A, B). 43. Terminalia from above. 44. Terminalia from below (magnification not stated).

Figs. 45-47.—*Embia gaillardi* Navás, holotype ♂. 45. Right forewing, × 10. 46. Terminalia from above, × 19. 47. Terminalia from below, × 19.

Figs. 48-52.—*Embia chudeaui* Navás, holotype ♂. 48. Head from above, × 35. 49. Right forewing, × 10. 50. Hind tarsus viewed laterally, × 35. 51. Terminalia from above, × 35. 52. Terminalia from below, × 35.

straight; left cercus-basipodite (LCB) with a small, slender, out-curved hook, arising from near the process of the hypandrium (HP).

♀ unknown.

Locality.—'Bassin du Moyen Niger: Bandiagara; R. Chudeau, 1909.'

Note.—In the Paris Museum is another male, identified by Navás as *E. chudeaui*; its label agrees, except that 'Doko' replaces 'Bandiagara'. It resembles the type superficially (size, colour, form of unprepared terminalia); time did not permit preparation and detailed examination of the terminalia.

E. chudeaui is probably the smallest winged species of *Embia*; this may be correlated with the weakening of the veins, especially Cu_{1a}. The structure of the terminalia, and especially the left cercus, is quite distinctive. The species obviously has no relationship to *Rhagadochir*.

Embia luridiceps Enderlein 1912. Fig. 53.

Coll. zool. de Selys-Longchamps, fasc. 3, p. 42, fig. 18.

♂ (after Enderlein). Length 7¼ mm.; length of forewing 6 mm., of hindwing 5¼ mm. General colour brown, head reddish-yellow, prothorax rust-red; wings brown, with broad hyaline inter-venal lines. Head rather narrow, sides behind eyes almost straight, weakly convergent, hind angles rounded. Wings with an extra vein apparent between cubital stem and its anterior branch ('Cu_2 im Vorder- und Hinterflügel kurz und mässig scharf'*). Terminalia (Fig. 53, after Enderlein, 1912, fig. 18) with process of left hemitergite relatively longer and thinner than in *E. savignyi*; first segment of left cercus with distal half of inner margin swollen as a rounded echinulate lobe; left cercus-basipodite apparently incurved in an acute hook.

♀ unknown.

Locality.—Eritrea: Asmara (Mus. Stettin, type).

Enderlein's figure is of a specimen somewhat distorted in preparation. There is possibly a significant difference, in the form of the left cercus, from *E. collarigera* End. (infra); the other differences apparent from the figures are probably due to distortion (cf. Enderlein, l.c.).

Embia collarigera Enderlein 1909. Fig. 54.

Embia collariger Enderlein, 1909, *Zool. Anz.*, 35, p. 182.—*Embia collarigera* Enderlein, Krauss, 1911, *Zoologica*, Hft. 60, Bd. 23, p. 67; Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, p. 109, 116.

Enderlein's original spelling '*collariger*' was summarily changed by Krauss to '*collarigera*', for agreement. If originally intended as a noun (cf. *Metoligotoma pugionifer* Davis), there seems little need for this change, but as Enderlein, after seeing Krauss's work, has (1912, Nachtrag) adopted the amended spelling, it may be retained.

♂ (after Enderlein, 1912, p. 41, fig. 17). Length 11·5 mm.; head 2·5 mm. × 2·0 mm.; length of forewing 9 mm., of hindwing 8 mm. General colour black, prothorax, underside and posterior half of dorsal surface of head, rust-red; wing-veins and bordering bands dark brown, with strong hyaline inter-venal lines. Head and wings as in *E. luridiceps*, i.e. cubitus with a weak branch between Cu_{1a} and stem. Terminalia (Fig. 54, after Enderlein, 1912, fig. 17) similar to

* Enderlein labels the vein called Cu_{1b} herein 'Cu_{st}'; an additional vein or trace between the anterior branch (Cu_1 or Cu_{1a}) and Cu_{st}, is labelled Cu_2.

E. luridiceps End., the first segment of the left cercus with a longer echinulate lobe, the acute termination of the left cercus-basipodite curved outwards.

♀ unknown.

Locality.—Adua, Ethiopia (type in Mus. Stettin).

The differences from *E. luridiceps*, over which this species has priority, seem very slight. There is agreement in the unusual colour and venation, and the localities are adjacent. The differences in the terminalia are exaggerated in Enderlein's figures, due to distortion in preparation; the constancy of the form of the left cercus in specimens from the type localities of the respective 'species' requires investigation.

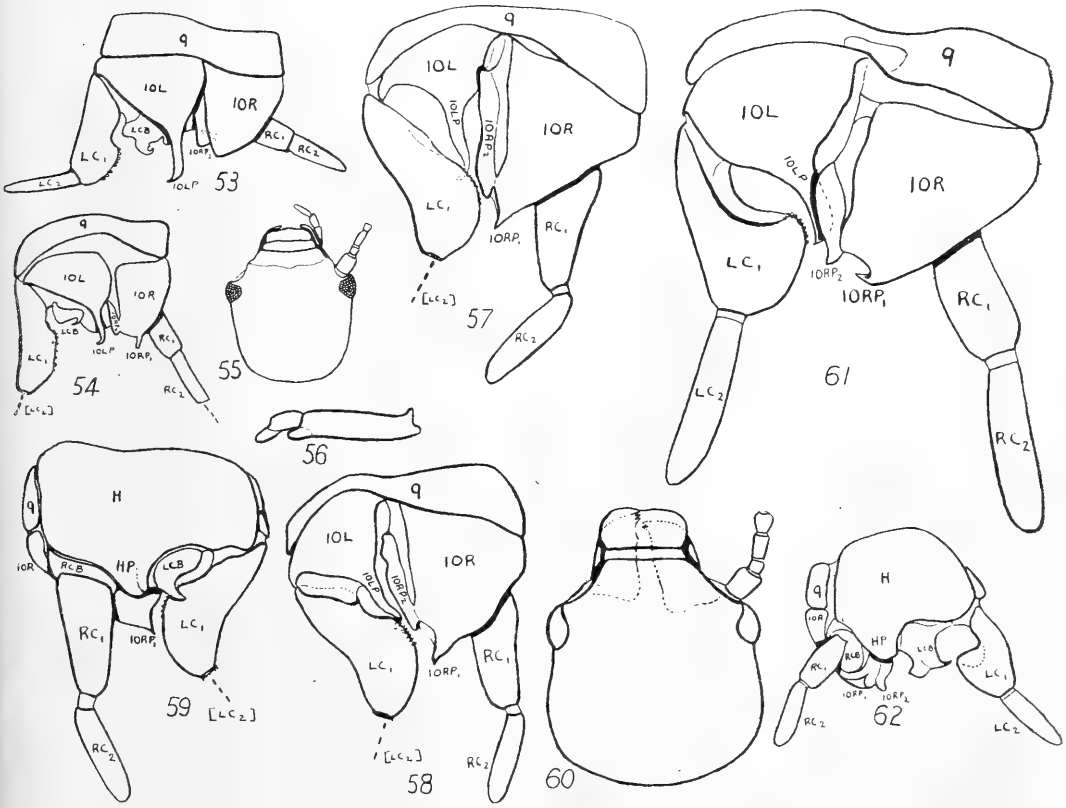


Fig. 53.—*Embia luridiceps* Enderlein, holotype ♂ (after Enderlein, 1912, fig. 18). Terminalia from above (distorted), × 19.

Fig. 54.—*Embia collarigera* Enderlein, holotype ♂ (after Enderlein, 1912, fig. 17). Terminalia from above (distorted), × 12.

Figs. 55-59.—*Embia femorata* Navás, holotype ♂. 55. Head from above, × 9. 56. First two segments of hind tarsus, viewed laterally, × 23. 57-58. Terminalia from above, slightly different aspects, × 23. 59. Terminalia from below, × 23.

Figs. 60-62.—*Embia verhoeffi* Friederichs, ♂ from Caia, Zambesi. 60. Head from above, × 23. 61. Terminalia from above, × 45. 62. Terminalia from below, × 23.

EMBIA FEMORATA Navás 1916. Figs. 55–59.

Mem. R. Acad. cienc. y artes de Barcelona, 12, no. 13, p. 22.

The following re-description is from the unique type (Mus. Congo):

♂. Length 10·5 mm.; head 2·3 mm. × 1·9 mm.; forewing 9·5 mm. × 2·0 mm.; hindwing 8·0 mm. × 2·5 mm. General colour dark brown, prothorax and all femora orange-brown, proximal abdominal tergites paler than rest of body, head especially dark, eyes black; wing-veins dark brown, bordered by smoky-brown bands. Head (Fig. 55) with eyes rather small, sides behind eyes weakly convergent, rounded behind. Antennae incomplete. Venation: According to my somewhat hasty notes, the venation is normal for the genus, *i.e.* the cubitus has not the extra branch found in *E. luridiceps* and *E. collarigera*, closely related species. This point requires checking. R_{4+5} with fork longer than stem; cross-veins rather numerous; no aberrations. Hind tarsi (Fig. 56) with only one metatarsal bladder, the metatarsus longer than in *E. savignyi*, *E. mauritanica*, etc. Terminalia (Figs. 57–59) agreeing closely with *E. collarigera* and *E. luridiceps*; process of left hemitergite (10LP) less acute terminally, and more sinuous; first segment of left cercus (LC_1) with inner echinulate dilation occupying central one-third of segment; left cercus-basipodite (LCB) curved outward, acute.

♀ unknown.

Locality.—Mufungwa Sampwe, Congo, 1–16.xii.1911, Dr. Bequaert.

Further research may prove that this species, *E. collarigera* and *E. luridiceps* are synonymous, or that they are races of one species. The present figures (57–59) cannot be compared closely with Enderlein's figures of the other species (54, 53), as the latter are made from distorted terminalia.

EMBIA VERHOEFFI Friederichs 1907. Figs. 60–62.

Verh. Zool. bot. Ges. Wien, 57, p. 273.

This species has been well re-described from the type (Portuguese East Africa; Mus. Berlin) by Enderlein (1912, p. 43, fig. 19). Friederichs (1923, p. 11, and Pl. i, fig. 1) gives a further figure of the type, showing the structure of the head, and the venation.

The following description is of two males from Caia, Zambesi (coll. H. Swale, on flowers, 15.7.1911; British Museum), which agree in all respects with the descriptions and figures cited above.

♂ (dry). Length 9–11 mm.; head 1·6 mm. × 1·3 mm.; forewing 6·0–7·5 mm. × 1·3–1·7 mm.; hindwing 5·0–6·5 mm. × 1·3–1·7 mm. (The type, after Enderlein, l.c., is slightly larger: Length 11·5 mm., length of forewing 9 mm., of hindwing 8 mm.) General colour dark brown, eyes black, prothorax orange-brown, rather bright. Wings with dark brown veins bordered by smoky-brown bands, intervenal lines broad, hyaline. Head (Fig. 60) broad, slightly expanded behind eyes, which are relatively small. Wings with fork of R_{4+5} subequal to stem in length; cubitus two-branched as in *E. mauritanica*. Hind tarsi as in *E. savignyi*, etc. Terminalia (Figs. 61–62) with posterior process of right hemitergite ($10RP_1$) short and acute, directed inward; process of left hemitergite (10LP) rather short and broad, acute, curved slightly to the left. First segment of left cercus (LC_1) very characteristic, third quarter dilated inward, echinulate; inner margin basad to dilation strongly excavate longitudinally, and concave in dorsal view. Left cercus-basipodite (LCB) curved to the left into an acute process, and with a flat lobe on the right directed towards the process of the hypandrium (HP). Other structures as throughout the genus.

♀. A very large female (length, dry, 20 mm.; head 3·2 mm. × 2·5 mm.), in the British Museum (Caia, Zambesi, 28.6.11, H. Swale), may possibly be referable to this species; this may be doubted from the colour (brown, prothorax concolorous). It is the largest member of the Order seen by me.

Locality.—Portuguese East Africa, coll. W. Tiesler (type ♂, Mus. Berlin); Caia, Zambesi (2 ♂, British Museum).

EMBIA SABULOSA Enderlein (1908). Figs. 63–66.

Olyntha sabulosa Enderlein, 1908, *Denkschr. med. naturw. Ges. Jena*, 13, p. 347, figs. 1–2.—*Embia sabulosa* Enderlein, 1909, *Zool. Anz.*, 35, p. 180; Krauss, 1911, *Zoologica*, 23, Hft. 60, p. 65; Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 45, figs. 21–22.

♂ (after Enderlein, 1912). Length 7·5–8·5 mm.; head 1·6 mm. × 1·1 mm.; forewing 5·5 mm. × 1·5 mm.; hindwing 5·1 mm. × 1·5 mm. General colour black, some sclerites dark brown (antennae, cerci, anterior parts of abdomen); wings with dark brown veins bordered by rather dark brown bands, inter-venal lines narrow, hyaline. Wings as in *E. mauritanica* (cf. Enderlein, 1912, fig. 23). Terminalia (Fig. 63, after Enderlein, 1912, fig. 22) similar to *E. savignyi*; process of left hemitergite (10LP) slightly longer and less curved, first segment of left cercus (LC_1) with inner dilation rather sharp, with a longitudinal channel basally.

♀ (after Enderlein, l.c.). Length 10–11 mm.; general colour dark brown.

Locality.—Kubub, Great Namaqualand, S.W. Africa. (types in Berlin and Stettin Museums).

In the British Museum is a male labelled 'S.W. Africa. Ovamboland. Kunene River (S. bank). March 1923. K. H. Barnard.' It appears to be referable to *E. sabulosa*. It approaches *E. savignyi* rather more closely than do the types (to judge from Enderlein's figures); this, and its more northerly locality, suggest that *E. sabulosa* may be a southern race of *E. savignyi*. Full particulars are as follows:

Length 10·5 mm.; head 1·9 mm. × 1·5 mm.; forewing 7·5 mm. × 1·7 mm.; hindwing 6·5 mm. × 1·7 mm. General colour very dark brown. Head (Fig. 64) with rather small eyes, sides behind eyes sinuous. Wings as in the types, except that M is clearly forked in the left forewing. Terminalia (Figs. 65–66) as in Enderlein's figure of a typical example, but with the inner face of the first segment of the left cercus (LC_1) smoother. The apparent differences in the right hemitergite (cf. Figs. 63, 65) are probably due only to orientation at the time the figures were prepared.

EMBIA PRODUCTA, n. sp. Figs. 67–69.

♂. Length 9 mm.; head 2·0 mm. × 1·7 mm.; forewing 7 mm. × 2 mm.; hindwing 6 mm. × 1·8 mm. General colour very dark brown, eyes black, wing-veins dark brown bordered by dark smoky-brown bands. Head (Fig. 67) similar in general outline to *E. mauritanica*, slightly narrowed behind eyes. Antennae with 25 segments, length 5 mm. Wings as in *E. mauritanica*; tarsi normal for the genus. Terminalia (Figs. 68–69) similar to *E. savignyi*, but with the first segment of the left cercus (LC_1) produced inwards medially to a strong echinulate beak, longer than thick, obtusely rounded terminally.

♀ unknown.

Locality.—Mogadiscio, Italian Somaliland, iv.1937, N. Cambiaso (holotype ♂, Museo Civico di Storia Naturale, Genoa).

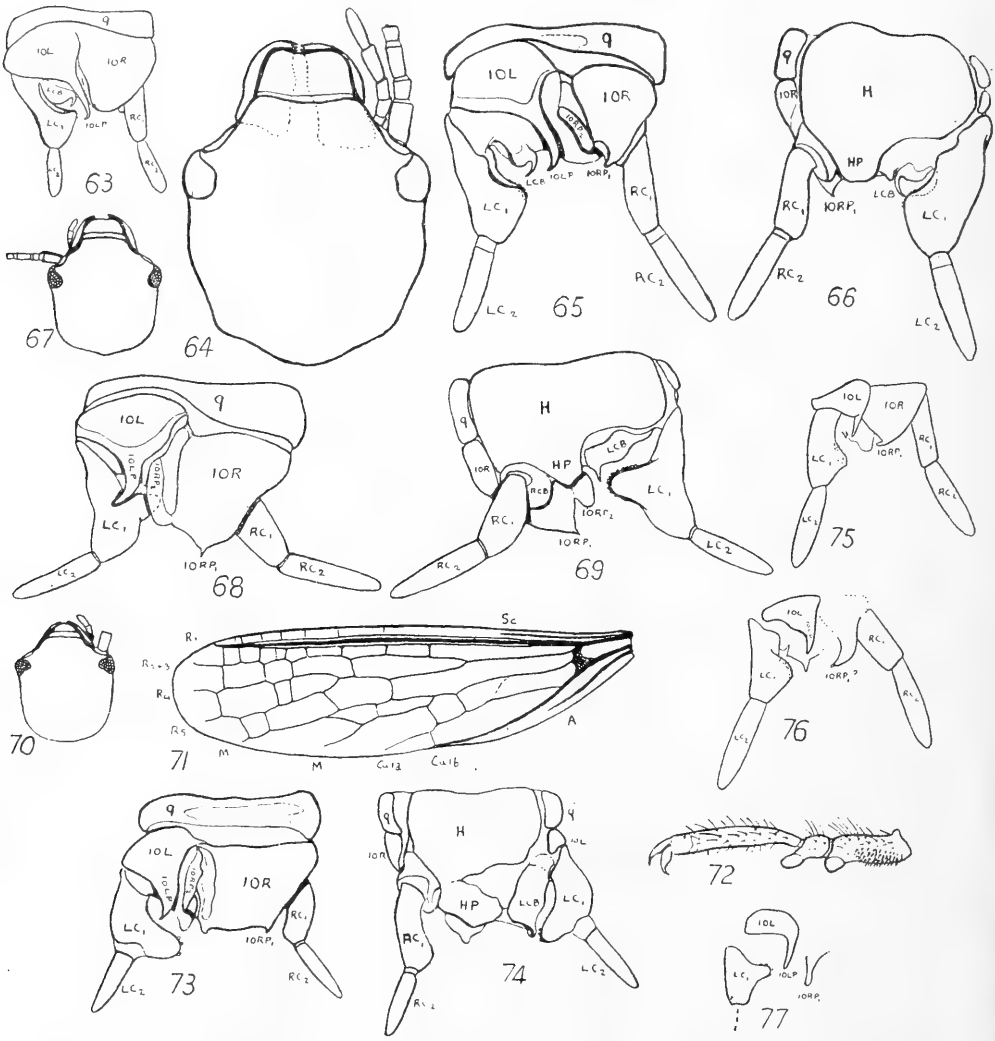


Fig. 63.—*Embia sabulosa* Enderlein, type ♂ (after Enderlein, 1912, fig. 22). Terminalia from above, × 18.

Figs. 64-66.—*Embia sabulosa* Enderlein, ♂ from Ovamboland. 64. Head from above, × 23. 65. Terminalia from above, × 23. 66. Terminalia from below, × 23.

Figs. 67-69.—*Embia producta* n. sp., holotype ♂. 67. Head from above, × 9. 68. Terminalia from above, × 23. 69. Terminalia from below, × 23.

Figs. 70-74.—*Embia ramosa* Navás, holotype ♂. 70. Head from above, × 9. 71. Left forewing, × 9. 72. Hind tarsus viewed laterally, × 32. 73. Terminalia from above, × 17. 74. Terminalia from below, × 17.

Fig. 75.—*Embia aethiopicorum* Karsch, holotype ♂ (after Enderlein, 1912, fig. 16). Terminalia from above (distorted), × 11.

Fig. 76.—*Embia camerunensis* Verhoeff, holotype ♂ (after Enderlein, 1912, fig. 20). Terminalia from above (distorted), × 17.

Fig. 77.—*Embia dissimilis* Rimsky-Korsakov, holotype ♂ (after Rimsky-Korsakov, 1924). Parts of terminalia from above. Magnification not stated.

The structure of the left cercus clearly differentiates this species from *E. savignyi*, which is related structurally on other characters, and which has an adjacent geographic range.

EMBIA RAMOSA Navás 1923. Figs. 70–74.

Rev. Acad. Cienc. Zaragoza, viii, p. 11, fig. 2.

The following re-description is from the unique type (Mus. Paris):

♂. Length 11 mm.; head 1·8 mm. × 1·5 mm.; forewing 8 mm. × 1·8 mm.; hindwing 7 mm. × 1·8 mm. General colour very dark brown, wings dark smoky-brown with hyaline inter-venal lines. Head (Fig. 70) much as in *E. producta*. Wings with R_{4+5} forked, M forked in left forewing (Fig. 71), simple in other wings; cross-veins numerous, one oblique, joining branches of M, in left forewing; anterior branch of cubitus (Cu_{1a}) simple, but with a cross-vein terminally connecting it to the stem (Cu_{1b}) in left forewing and right hindwing; in the right hindwing an oblique cross-vein also connects Cu_{1a} to M, and resembles an extra anterior branch of Cu_{1a}. Tarsi (Fig. 72) as in *E. savignyi*. Terminalia (Figs. 73–74) more aberrant than any other species included in *Embia*; inner process of right hemitergite ($10RP_2$) with a small triangular sclerite distally; posterior border of right hemitergite (10R) broad and concave between $10RP_2$ and posterior process ($10RP_1$). Process of left hemitergite (10LP) very broad, tapered, subacute, slightly curved to the left, not delimited from the body of the hemitergite (10L) by any boundary. First segment of left cercus (LC_1) terminally produced inward to a long obtuse lobe, with a few (some 3–4) small nodules terminally. Hypandrium (H) with a broad posterior process (HP), separated from H in its left-hand part by membrane (possibly due to breakage); left cercus-basipodite (LCB) tapered posteriorly, obtuse, rotated about longitudinal axis.

♀ unknown.

Locality.—Mozambique: 'Vallée du Revoué, env. d'Andrada, G. Vasse, 1905, Octobre.'

This species is possibly distinct from *Embia*, at least subgenerically.

Species insufficiently known.

The following three species, from Johann-Albrechts-Höhe, Cameroons, are very probably synonymous, but the existing figures do not decide this point with certainty, nor do they give a clear picture of the relationship to other species:

EMBIA AETHIOPICORUM Karsch, 1900, *Ent. Nachr.*, 26, p. 79.

The terminalia have been figured by Enderlein (1912, fig. 16, from the type ♂, Mus. Berlin); this figure is reproduced here (Fig. 75); the various parts of the terminalia are obviously much distorted. Verhoeff (1904, Pl. 3, fig. 16) gives a careful figure of part of the terminalia of the type; the left cercus-basipodite is suggestive of *E. tunetana* Nav.

EMBIA CAMERUNENSIS Verhoeff, 1904, *Abh. Leop.-Carol. Ak. Naturf. Halle*, Bd. 82, p. 202.

The terminalia of the type ♂ (Mus. Berlin) have been figured by Enderlein (1912, fig. 20; reproduced here, Fig. 76). The same remarks apply as to *E. aethiopicorum*. Verhoeff's figure of the left hemitergite (l.c., Pl. 4, fig. 24) tends to emphasize the structural similarity to *E. aethiopicorum*. Verhoeff apparently differentiated *E. camerunensis* from this species by size only.

EMBIA DISSIMILIS Rimsky-Korsakov, 1924, *Ent. Mitt.*, xiii, 1, p. 5, figs. a–c.

Rimsky-Korsakov's figures of the terminalia (reproduced here, Fig. 77) do not seem to have been made with his usual care and accuracy. It is difficult to compare the figure with either of the above. The type is probably in the Berlin Zoological Museum; the data are: 'L. Conradt, N. Kameroons, Johann-Albrechts-Höhe, 1896.' Rimsky-Korsakov notes that it resembles *E. aethiopicorum*, but is smaller, and the terminalia differ from Enderlein's figure of that species.

It is possible that over-maceration of the specimens figured by Enderlein accounts for their difference *inter se*, and for the difference in the left cercus from Rimsky-Korsakov's figure. The synonymy and true structure of this series may be decided by future research. The differences in length of the types of the three 'species' (15 mm., 10 mm., 8 mm.) do not represent a greater difference than that noted in Lucas's single type series of *E. mauritanica*; the general colour of the three specimens (dark brown) offers no basis for distinction, even if colour could be allowed as a taxonomic criterion in this Order.

Species incorrectly referred to Embia.

Many species incorrectly referred to *Embia* have been dealt with already in this series. The following Neotropical species, not yet considered, are generically distinct, and will be considered in the next part of this series:

Embia brasiliensis (Griffith and Pidgeon) Enderlein, *E. ruficapilla* (Burmeister) Enderlein, *E. klugi* Rambur, *E. mülleri* Hagen, *E. batesi* M'Lachlan, *E. salvini* M'Lachlan, *E. birabeni* Navás, *E. wagneri* Navás, *E. piquetana* Navás.

Unrecognizable species.

The following species, whilst probably referable to *Embia*, are unrecognizable specifically on the existing descriptions:

Embia kraussi Krausse, 1911, *Int. Ent. Zeitschr.* (*Guben*), v, 9, p. 64.—This species was described from females and larvae from Asuni, Sardinia. It might be established by collection of males from that locality, but may well prove synonymous with *E. ramburi* R.-Kors. (see also Rimsky-Korsakov, 1924, p. 5, and Friederichs, 1934, p. 409).

Embia kraussi Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 113.—Described from a female from Tanganyika, this species is of course unrecognizable, and is also a homonym.

Embia vayssièrei Navás, 1934, *Brotéria*, Série trimestral, iii, fasc. 1, p. 19.—Described from a female, this species is unrecognizable; it may possibly be established by the collection of males from the exact locality (Senegal: M'Bambey; cf. Vayssière, 1934, who states that the insect is very common in this locality).

Embia smaeleni Navás, 1923, *Rev. Acad. Cienc. Zaragoza*, viii, p. 12.—This species was erected on a male, from Elisabethville, Congo, of which the abdomen was lacking. As numerous species of Embioptera inhabit this territory, the species can hardly be established, even by examination of the defective type (reputed to be in Navás's Collection), as, lacking the terminalia, it is unlikely that it could be identified with further specimens collected from the type locality, if such a series could be obtained.

Embia femoralis Navás, 1931, *Rev. Zool. Bot. africaines*, 21, fasc. 2, p. 133.—There is nothing in Navás's description of this specimen, from the Congo, to distinguish it from *E. femorata* Navás 1916 (supra), also from the Congo. It is probably synonymous, as well as nearly homonymous. The type (Mus. Congo) requires examination to decide this point.

Embia fuentei Navás, 1918, *Mem. R. Acad. cienc. y artes de Barcelona*, xiv, no. 4, p. 22 (358).—The species is unrecognizable from Navás's description. The locality is Pozuelo de Calatrava, Ciudad Real, Spain; the type ♂ is (or was) in Navás's Collection. It may be conspecific with a male (Mus. Madrid), also winged, from Cartagena, Spain, determined by Krauss (1911, p. 62) as *E. mauritanica* Lucas.

Full details of winged specimens from this region, especially of the terminalia, would be of interest. They may represent winged forms of species now only known as wingless (e.g. *E. ramburi* R.-Kors.).

Note.—In view of the fact that the specific differences in this genus are represented by slight variations in shape of the components of the complex terminalia, no satisfactory verbal key to the species can be prepared. This emphasizes the absolute necessity for accurate figures of the terminalia in future descriptions of new species.

It would be premature at the present stage to enter into any detailed discussion of the relationships of the different species, especially as so many of the facts, particularly those relating to the Circum-Mediterranean species, are at present in a very vague state.

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XVII. A NEW NEOTROPICAL GENUS PREVIOUSLY CONFUSED WITH EMBIA LATREILLE.

(Forty-one Text-figures.)

Genus EMBOLYNTHA, n. gen.

Genotype, *Olyntha brasiliensis* Griffith and Pidgeon, 1832, The Animal Kingdom arranged in conformity with its Organization, by the Baron Cuvier, with Supplementary Additions to Each Order, Vol. 15 (Insects, Vol. 2), p. 347.—(*Embius* ? *brasiliensis* Griffith and Pidgeon 1831, Pl. 72 of the above work, issued separately). Ex Gray MSS.—(*Embius?* Griffith and Pidgeon 1831, l.c. Not *Embia* Latreille 1829.—*Olyntha* Griffith and Pidgeon 1832, l.c. Not *Olynthus* Hübner 1818 (Coleoptera)).

Neotropical Embioptera, the males with the following characters: Winged, R_1 usually confluent subterminally with R_{2+3}; R_{4+5} forked; M simple; Cu_{1a} simple. All veins well developed, cross-veins rather numerous. First segment of hind tarsus with a terminal ventral bladder, and with a rather small conical bladder medially on the ventral surface. Tenth abdominal tergite completely divided longitudinally; right hemitergite with inner margin produced forward towards ninth tergite as a heavily-sclerotized lobe (not, as in *Embia*, with a flat elliptical flap of chitin separated except at posterior limit by membrane). Process of left hemitergite simple (i.e. not bifid, though it may carry accessory spines). Inner margin of left hemitergite, basad to process, bearing to the left before reaching ninth tergite. First segment of left cercus with a prominent echinulate lobe on inner margin. Second segment of each cercus long and rather thin, but liable to appear thicker by flattening and distortion.

The genus differs from *Embia* in the hind tarsi and in the terminalia; the latter have reached a stage of specialization from more generalized ancestors somewhat similar to that reached by *Embia*, but are, in detailed structure, clearly separable generically.

An additional difference, noted by Griffith and Pidgeon (l.c.) and Westwood (1837, p. 373), is that the antennae are very much elongated (in *Embia*, less than 26 short segments, usually about 20; in *Embolyntha*, approximately 30, segments longer). This is of little use as a criterion for preserved specimens, as the antennae are usually broken.

Griffith and Pidgeon (l.c.) noted that the segments of the maxillary palps are broader than in *Embia*. This difference seems to apply only to the genotype, *E. brasiliensis*, being therefore specific rather than generic. Westwood (1837, p. 373) incorrectly states that this species has 4-segmented maxillary palps.

EMBOLYNTHA BRASILIENSIS (Griffith and Pidgeon 1831–2). Figs. 1–7.

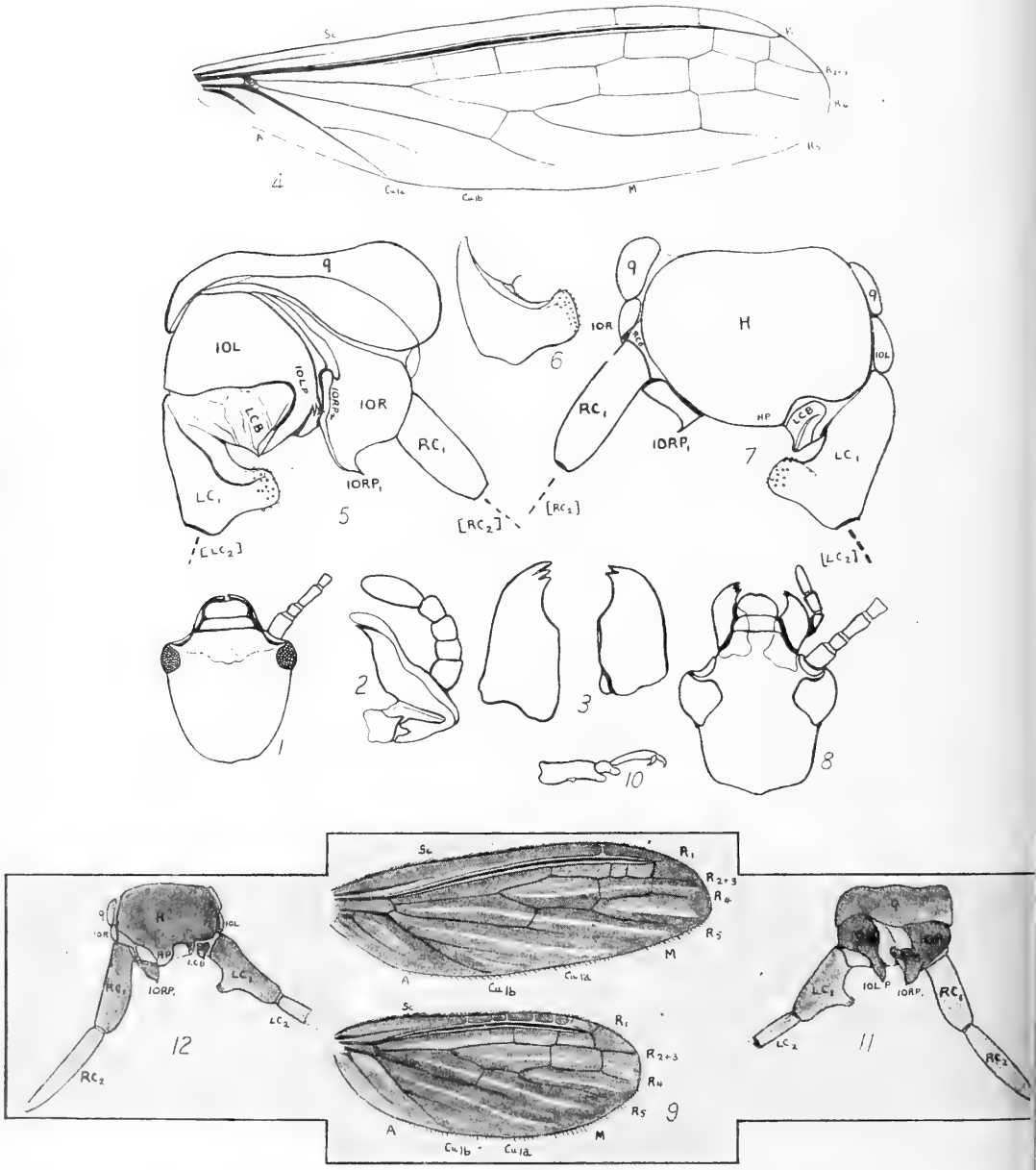
Olyntha brasiliensis Griffith and Pidgeon 1832, l.c. (*Embius ? brasiliensis* Griffith and Pidgeon 1831, l.c.).

♂ (holotype, Children Collection, British Museum of Natural History). Length 15 mm.; head 2·9 × 2·4 mm.; hindwing 11 × 3 mm.; end of forewing abraded, breadth as for hindwing. General colour (dry) dark chocolate-brown, prothorax and forelegs (except tibiae and tarsi) orange-brown, wing-veins dark brown with bordering bands mid-brown, inter-venal lines hyaline. Head (Fig. 1) with sides behind eyes convergent, rounded. Right antenna incomplete; left 11 mm. long, with 32 segments. Maxilla (Fig. 2) with 5-segmented palp, segments rather thicker than in other members of the Order. Mandibles incurved, the left with three, the right with two acute teeth (Fig. 3). Wings (Fig. 4) as in the generic description. Hind legs missing; the tarsal bladders are presumably the same as in related species (infra). Terminalia (Figs. 5–7) with right hemitergite (10R) produced posteriorly to an acute process ($10RP_1$), directed outward and downward; inner margin of 10R produced forward, and thickened, as a strong lobe ($10RP_2$), rounded in front. Left hemitergite (10L) produced inward, curving round posteriorly to an acutely-tapered process (10LP). Two minute hooks arise basally from the inner margin of 10LP. First segment of right cercus (RC_1) subcylindrical, arising from a small basipodite (RCB); second segment now lacking in both cerci of the type, subcylindrical according to the early figures of this specimen (l.c.). First segment of left cercus (LC_1) produced inward subterminally in a strong, rather square, echinulate lobe; inner margin, basad to lobe, longitudinally grooved. Hypandrium (H) smoothly rounded posteriorly, with a small bay on the left-hand side of the posterior margin, in which is lodged the left cercus-basipodite (LCB). LCB obtusely tapered behind, chitinization weakened in a median longitudinal membraneous slit.

♀ unknown.

Locality.—Brazil (detailed locality not known).

Note.—The specimen (♂) figured by Enderlein (1912, fig. 24) as *Embia brasiliensis* seems to be conspecific; differences in Enderlein's figure may be due to the personal equation in figuring. Enderlein's identification seems to have been a lucky coincidence, as he had not seen the type, and the original description contains nothing to differentiate it from other Neotropical species. The locality of Enderlein's specimen is Brazil (detailed locality not known).



Figs. 1-7.—*Embolyntha brasiliensis* (Griffith et Pidgeon), holotype ♂. 1. Head from above, × 8. 2. Right maxilla from above, × 20. 3. Mandibles from above, × 20. 4. Right hindwing, × 7. 5. Terminalia from above, × 20. 6. First segment of left cercus viewed more from the left, × 20. 7. Terminalia from below, × 20.

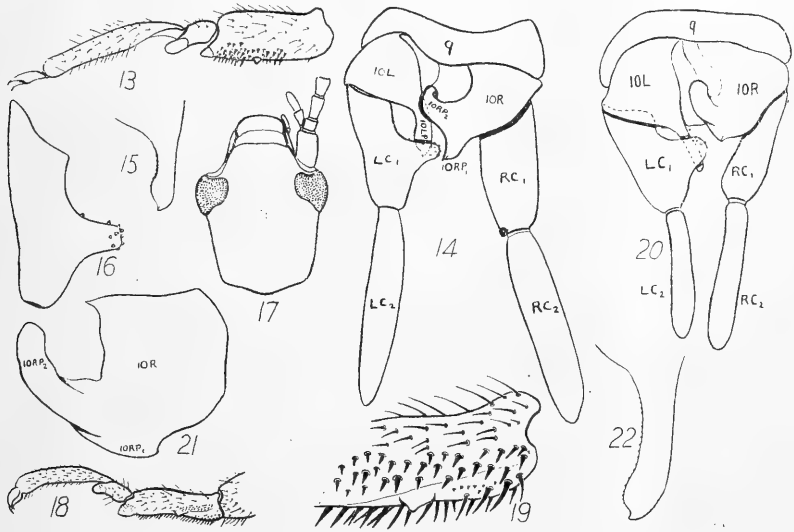
Figs. 8-12.—*Embolyntha batesi* (M'Lachlan), holotype ♂. 8. Head from above, × 20 (slightly distorted by flattening). 9. Right fore- and hindwing, × 8. 10. Hind tarsus viewed laterally, × 20. 11. Terminalia from above, × 20. 12. Terminalia from below, × 20.

EMBOLYNTHA BATESI (M'Lachlan 1877). Figs. 8–27.

Embia batesi M'Lachlan, 1877, *J. Linn. Soc. London*, Zool., xiii, no. 70, p. 380.

The following re-description is from the holotype ♂ (M'Lachlan Collection, British Museum of Natural History):

♂. Length 9 mm.; head 1·4 × 1·1 mm.; forewing 6·5 × 2·2 mm.; hindwing 5·5 × 2·2 mm. General colour very dark brown; wings with dark brown veins bordered by broad smoky-brown bands, inter-venal lines narrow, hyaline. Head (Fig. 8) with large prominent eyes; sides behind eyes converging posteriorly, smoothly rounded behind. Mandibles as in *E. brasiliensis*; segments of maxillary palps less thickened. Antennae incomplete, the left with 18 segments (last three pale). Wings (Fig. 9) very broad, with a fringe on posterior margin; venation normal for the genus, except that R_1 is not terminally confluent with R_{2+3}, but gives off a twig to the margin, and a strong cross-vein to R_{2+3}. Right forewing of type with a second anal vein. Hind tarsi (Fig. 10) as in generic diagnosis. Terminalia (Figs. 11–12) with posterior process of right hemitergite ($10RP_1$) broad, tapered,



Figs. 13-16.—*Embolyntha batesi* (M'Lachlan), ♂ from Espirito Santo, Brazil (M'Lachlan Collection). 13. Hind tarsus viewed laterally, × 42. 14. Terminalia from above, × 30. 15. Process of left hemitergite from above, × 42. 16. First segment of left cercus from above, × 42.

Figs. 17-22.—*Embolyntha batesi* (M'Lachlan), ♂ from Barro Alto, Brazil (Museum of Comparative Zoology). 17. Head from above, × 12. 18. Hind tarsus viewed laterally, × 22·5. 19. Basal half of first segment of hind tarsus, viewed laterally, × 48. 20. Terminalia from above, × 22·5. 21. Right hemitergite from above, × 48, posterior process curved down, partly concealed. 22. Process of left hemitergite from above, × 48.

(All figures based on camera lucida outlines except Figs. 38-41, which were prepared with constant use of an ocular micrometer. Conventional lettering for venation. Setae omitted except in Figs. 13, 18, 19, and the wing-fringe of Fig. 9. Shading in Fig. 9 to represent pigmentation; shading or stippling in Figs. 11, 12, 29 and 31 to represent degree of sclerotization and pigmentation. 9, ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, $10RP_2$, posterior and inner processes of 10R; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; H, hypandrium; HP, process of H.)

directed inward and backward; inner process ($10RP_2$) a broad rounded knob directed forward, slightly incurved terminally. Left hemitergite (10L) produced back to a rather broad, tapered process (10LP), subacute, slightly expanded subterminally. Right cercus with two elongate subcylindrical segments (RC_1, RC_2); right cercus-basipodite small, distally largely membraneous. First segment of left cercus (LC_1) with inner margin medially produced to a prominent obtuse beak, armed with about ten nodules; second segment (LC_2) subcylindrical (damaged in type). Hypandrium (H) produced backward to the right of the mid-line to a blunt process (HP); space between HP and base of LC_1 membraneous, with a small bar projecting from the hypandrium, and a distinct basipodite (LCB), subtriangular, terminally acute.

♀ unknown.

Locality.—Brazil ('Amazons', after M'Lachlan; exact locality uncertain); coll. Bates.

Variation and Distribution.—A series of males in the M'Lachlan Collection,* from Espirito Santo (Brazil), are referable to this species. The details of this series are: Length 9·8–10·5 mm.; head 1·5–1·6 × 1·2 mm.; forewing 9·2–9·8 × 2·5–2·7 mm.; hindwing 7·5–7·8 × 2·4–2·6 mm. General colour dark golden-brown, head, meso- and metascutum, and legs, paler, eyes black, wings as in the type. Hind tarsus (Fig. 13) and terminalia (Figs. 14–16) as in the type. The antennae are up to 6·4 mm., with up to 23 segments.

In the Museum of Comparative Zoology, Harvard University, are two males (Barro Alto, Est. Minas, Brazil, coll. José Blaser, —.xi.1931). They are slightly larger than the specimens detailed above (length 11–13 mm.; head 1·8–2·0 × 1·4–1·5 mm.; forewing 9·5–10·0 × 2·2–2·5 mm.), and the head (Fig. 17) somewhat narrower, but the colour, venation, hind tarsi (Figs. 18–19), and terminalia (Figs. 20–22) agree closely. The antennae are incomplete, but even so reach a length of 7·5 mm. (22 segments).

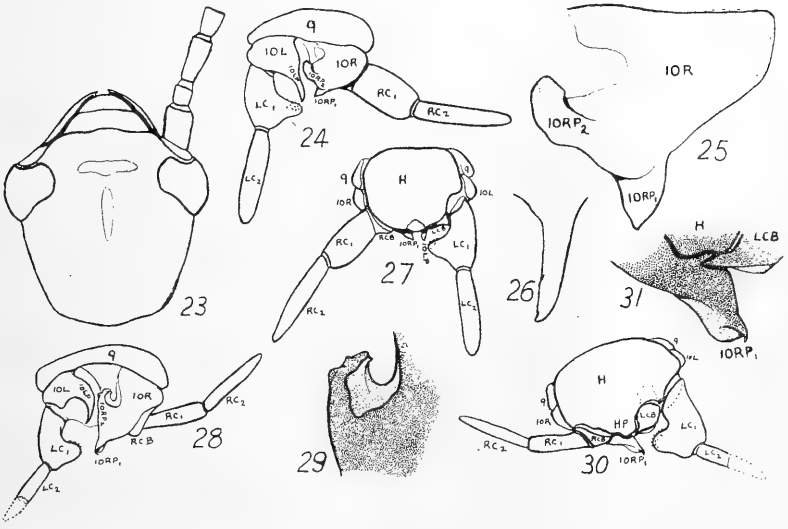
The male from which Enderlein (1912, p. 49, figs. 25–26) re-described *Olyntha ruficapilla* Burmeister (1839, Handbuch der Entomologie, vol. ii, p. 770), is from San Joâo del Rey, Brazil (Mus. Berlin). It shows some similarity to the present species. Burmeister's original description was merely 'Fusca, capite cum pronoto rufo; alis albo-striatis; cercis fuscis; long. 3½. Brasilien'. Unless his original types (which may be at Halle) can be discovered and re-described, the name must remain unrecognizable.

Two males, from which Hagen (1885, pp. 176–178) re-described *Olyntha ruficapilla*, are in the Museum of Comparative Zoology. One is from Brazil ('from the collection of the late Dr. Schneider; . . . it may have belonged to the same lot with Burmeister's types and those in the Berlin Museum,† but it has not been compared with them'.—Hagen, l.c.); the other from Venezuela, coll. Appun. The former has some similarity to *E. batesi*, but is not identical; it agrees more closely with Enderlein's specimen (supra). The differences from *E. batesi* lie in the head (Fig. 23), which is more narrowed behind, and in the terminalia (Figs. 24–27), which have the process of the left hemitergite (10LP) evenly tapered (not slightly expanded subterminally as in the type of *E. batesi*), and the dilation of the first segment of the left cercus (LC_1) more distal in position.

* Not handled by M'Lachlan when his description was framed; he states (1877, p. 380): 'I have one example, collected by Mr. Bates on the Amazons'.

† Presumably the specimen from San Joâo del Rey (coll. Sello), described by Enderlein (supra). The identity with Burmeister's type series is merely conjecture.

Hagen's other specimen, from Venezuela, is not at all closely related to *E. batesi*, but in view of the fact that the head is missing, and the exact locality unknown, it should not be named. The terminalia (Figs. 28–31) have numerous points of difference; the inner process of the right hemitergite ($10RP_2$; Fig. 29) is roughened, somewhat reminiscent of the unrelated genus *Notoligotoma*; the posterior process of the right hemitergite ($10RP_1$; Fig. 31) has an acute out-curved extremity, and an obtuse subterminal flange on the right; the process of the left hemitergite (10LP; Fig. 28) is broad, curved, evenly-tapered, and acute terminally; and the first segment of the left cercus (LC_1) has the internal echinulate lobe massive and subterminal.



Figs. 23-27.—*Embolyntha batesi* (M'Lachlan), var., ♂ from Brazil. (Identified by Hagen as *Olyntha ruficapilla* Burmeister. Museum of Comparative Zoology.) 23. Head from above, × 20. 24. Terminalia from above, × 20. 25. Right hemitergite from above, × 70. 26. Process of left hemitergite from above, × 70. 27. Terminalia from below, × 20.

Figs. 28-31.—*Embolyntha* sp. indet., ♂ from Venezuela. (Identified by Hagen as *Olyntha ruficapilla* Burmeister. Museum of Comparative Zoology.) 28. Terminalia from above, × 20. 29. Inner process of right hemitergite, viewed from above, × 70. 30. Terminalia from below, × 20. 31. Posterior process of right hemitergite, and extremities of left cercus-basipodite and process of hypandrium, from below, × 70.

Embolyntha salvini (M'Lachlan 1877). Figs. 32-37.

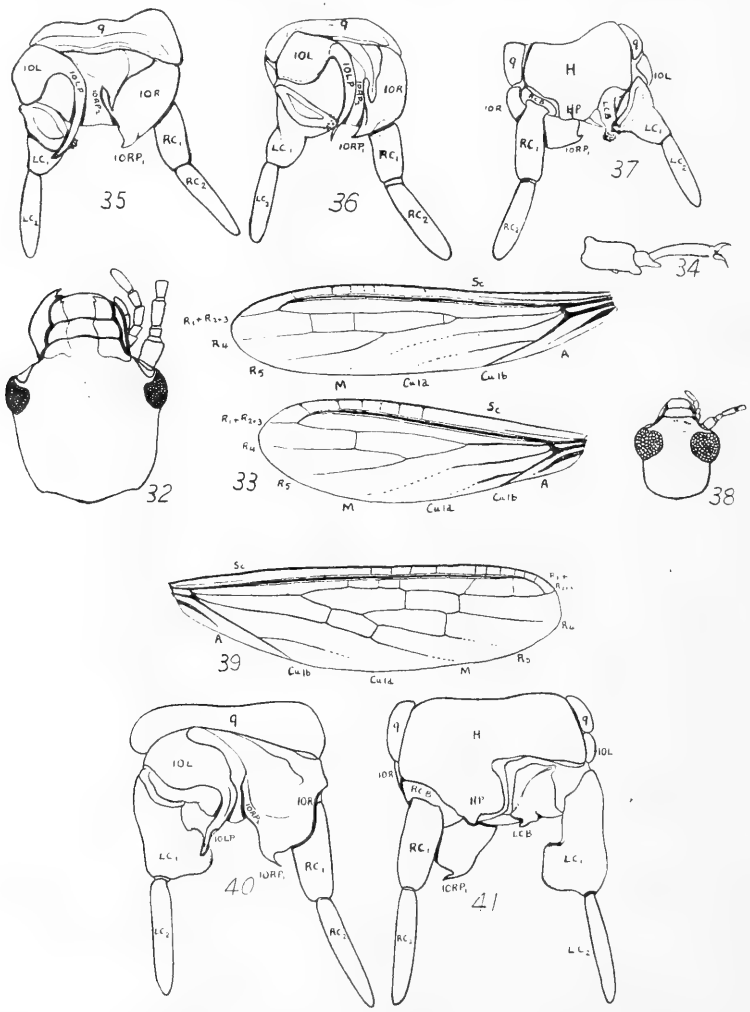
Embia salvini M'Lachlan,* 1877, *J. Linn. Soc. London*, Zool., no. 70, p. 380.

The following re-description is from the unique type (M'Lachlan Collection, British Museum of Natural History):

♂. Length 10·5 mm.; head 1·9 × 1·5 mm.; forewing 6·5 × 1·5 mm.; hindwing 5·5 × 1·7 mm. General colour black, some sclerites very dark brown; wings with dark-brown bands, hyaline inter-venal lines narrow. Head (Fig. 32) with eyes rather prominent, sides behind eyes rounded, converging posteriorly. Mandibles as in *E. brasiliensis* and *E. batesi*. Antennae incomplete. Wings (Fig. 33) narrow, veins arranged as in *E. brasiliensis*; cross-veins few; media and anterior branch of

* Enderlein (1912, p. 30) refers to *E. salomi*, a lapsus calami for *salvini* (corrected l.c., p. 116).

cubitus becoming obsolete terminally. Hind tarsi (Fig. 34) as in *E. batesi*. Terminalia (Figs. 35–37) very characteristic; posterior process of right hemitergite ($10RP_1$) directed inward, subacute; inner process ($10RP_2$) less massive than in *E. batesi*. Left hemitergite (10L) somewhat similar to *E. brasiliensis*, the process (10LP) longer and thinner, without hooks. Right cercus with two elongate subcylindrical segments (RC_1, RC_2), with a small annular basipodite (RCB). First segment of left cercus (LC_1) basally dilated internally in an obtuse



Figs. 32-37.—*Embolyntha salvini* (M'Lachlan), holotype ♂. 32. Head from above, × 15. 33. Left fore- and hindwing, × 8. 34. Hind tarsus viewed laterally, × 20. 35. Terminalia from above, × 20. 36. Terminalia from above and slightly to the left, × 20. 37. Terminalia from below, × 20.

Figs. 38-41.—*Embolyntha wagneri* (Navás), holotype ♂. 38. Head from above, × 8. 39. Right forewing, × 6. 40. Terminalia from above, × 20. 41. Terminalia from below, × 20.

echinulate lobe, distally smooth and subcylindrical; second segment (LC_2) subcylindrical. Hypandrium (H) produced to a blunt process (HP) to the right of the mid-line; left cercus-basipodite (LCB), between HP and base of LC_1, produced backwards, terminally slightly expanded into an echinulate lobe, lying adjacent to the echinulate lobe of LC_1.

♀ unknown.

Locality.—Chinautta, Central America, at 4100 ft., coll. Salvin.

EMBOLYNTHA WAGNERI (Navás 1923). Figs. 38–41.

Embia wagneri Navás 1923, *Rev. Acad. Cienc. Zaragoza*, viii, p. 13, fig. 3.

The following re-description is from Navás's unique type (Mus. Paris):

♂. Length 10 mm.; head 1·7 × 1·4 mm.; forewing 9 × 2·5 mm.; hindwing 8 × 2·4 mm. General colour dark ferruginous, eyes black; wings with R_1 dark brown, other veins golden-brown, bordered by bands of smoky mid-brown, hyaline inter-venal lines rather narrow. Head (Fig. 38) broad, eyes very large, prominent, almost circular in dorsal view; antennae approximately 6 mm. in length, the left with 25, the right with 24 segments. Wings (Fig. 39) as in *E. brasiliensis*. Hind tarsi missing in the type. Terminalia (Figs. 40–41) reminiscent of *E. brasiliensis*; right hemitergite (10R) with posterior process ($10RP_1$) acute, directed backward and to the right; inner margin of 10R sinuous, produced forward from $10RP_1$ as a thickened flange or lobe ($10RP_2$) as in *E. brasiliensis*. Left hemitergite (10L) as in *E. brasiliensis* and *E. salvini*; process (10LP) long, slender, sinuous, without hooks as in *E. brasiliensis*, terminally subacute. Right cercus with two subcylindrical segments (RC_1, RC_2), with a small annular basipodite (RCB). First segment of left cercus (LC_1) with a square echinulate subterminal lobe internally, broader than in *E. brasiliensis*; second segment (LC_2) elongate-subcylindrical. Hypandrium (H) produced back to a blunt, weakly-bilobed process (HP), to the right of the mid-line. Left cercus-basipodite (LCB), between HP and base of LC_1, represented by a flat plate, with an oblique medial membraneous slit as in *E. brasiliensis*; LCB distally obtuse, with a small lobe projecting inwards and upwards.

♀ unknown.

Locality.—Argentina: 'Chaco de Santiago del Estero. Bords du Rio Salado. La Paliso del Bracho. 25 kil. N.O. (N.W.) d'Icaño. E.-R. Wagner, Décembre, 1905.'

Key to the Species of Embolyntha (♂).

1. First segment of left cercus with a basal internal echinulate lobe; left cercus-basipodite terminally echinulate ..... *salvini* (M'Lachlan)
   Echinulate lobe of first segment of left cercus not basal; left cercus-basipodite not echinulate 2
2. Posterior process of right hemitergite slender, directed outward; internal echinulate lobe of first segment of left cercus subterminal 3
   Posterior process of right hemitergite short and thick, directed inward; internal lobe of first segment of left cercus medial (subterminal in non-typical variations) ..... *batesi* (M'Lachlan)
3. Process of left hemitergite carrying two small hooks; internal lobe of first segment of left cercus longer than thick ..... *brasiliensis* (Griffith & Pidgeon)
   Process of left hemitergite not as above; internal lobe of first segment of left cercus broader than long ..... *wagneri* (Navás)

Unrecognizable Species.

Olyntha ruficapilla Burmeister 1839.—This species has been discussed above (under *Embolyntha batesi*).

Embia klugi Rambur 1842, Histoire naturelle des Insectes, Névroptères, p. 313.—As far as can be said from the short description, this species may belong to *Embolyntha*; it cannot belong to *Embia*, because of the locality (Brazil). The type is apparently lost (it is not in the Paris Museum). The species must be deleted as unrecognizable.

Embia (*Olyntha*) *mülleri* Hagen, 1885, *Canad. Entomologist*, 17, p. 206.—The type, from Itajahy, Santa Cattarina, Southern Brazil, is in the Museum of Comparative Zoology, Harvard University. It is a dried female, labelled: 'Embiden larve. Itajahy, Brazil, 1879 Jr. (year). Mueller', and, in Hagen's writing, 'O. muelleri* Hag., Mon. Emb. p. 206, 17'. On account of its sex, it carries no specific characters; it may belong to *Embolyntha*, but it should be deleted as unrecognizable specifically.

Embia birabeni Navás 1918, *Brotéria*, Série Zoológica, xvi, p. 105, figs. 5*a-c*.—It is impossible to judge from Navás's description to which genus this species should be referred; it is probably referable to *Embolyntha*, possibly however to *Pararhagadochir*. Details of the left hemitergite are lacking; the posterior process of the right hemitergite seems to resemble *E. brasiliensis* and *E. wagneri*. Navás's figure of the first segment of the left cercus (l.c., fig. 5*a*) is merely a circle with a few lines representing setae; this is of course impossible. The type ♂, from Unquillo, Córdoba, Argentina (Mus. La Plata) requires re-examination. The species might possibly be synonymous with *E. wagneri* (Navás), also from the Argentine, which it would supersede by priority; but here, as in the case of *E. batesi*–*E. ruficapilla*, the certain name has been adopted in preference to the doubtful, though prior, name.

Embia piquetana Navás 1919. *Mem. Pont. Accad. Romana dei Nuovi Lincei*, Series ii, vol. 5, p. 25.—This species was described from a female from Santa Fé, Argentina. Of course, it cannot be recognized, as the females of this Order do not possess specific characters. The genus to which the specimen belonged may have been *Embolyntha*, or some other Neotropical genus. Navás's note (l.c.), that it is 'like *birabeni* Navás', resembles the blind leading the blind.

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A LISTROPHORID PARASITE OF THE WALLABY, FROM NEW GUINEA.

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

(Five Text-figures.)

[Read 31st July, 1940.]

About thirty of these parasites were taken from a wallaby at Bulolo, T.N.G. They were attached, head downwards, to the fine white hairs on the posterior part of the abdomen and the medial surfaces of the hind legs. Occasionally two specimens occupied the same hair.

There are two forms, presumably male and female, but there is no direct evidence as to which is which. Inside some of each appear large duplicates, occupying almost the whole of the body space; these have eight legs, and therefore cannot be larvae (apart from the fact that they are so large that they could only emerge by destroying the whole shell; and that they lie in the same direction as the containing shell, whereas the larvae in this genus lie in the opposite direction). It is assumed that they are forms undergoing metamorphosis within the nymphal skin of the previous stage; this assumption is apparently supported by the fact that frequently an empty skin, split along the mid-line of the abdomen, is found attached to a hair, with a complete specimen attached directly behind it.

Of these two forms, one is consistently larger, and shows distinct differences from the smaller form as regards the terminalia, and in the number, size, and arrangement of the body setae.

There is indirect evidence as to sex, however. Lawrence (*Parasitology*, xxx, 3, 1938, 309) has described specimens of *Labidocarpus nasicolus* from a bat, which contain hexapod embryos within the abdomen, and are therefore females. No males were taken. The general setological plan of these specimens corresponds almost exactly with that of the smaller New Guinea form, and therefore this form is here described, provisionally, as the female.

There is no apparent difference between a newly-emerged form and its preceding stage, as far as can be ascertained from an examination of the cast skin. Where a contained form can be compared with its intact outer skin, the terminalia appear to be identical in form. It is because of this that the specimens are described as last-stage nymphs and/or young adults, since it is most likely that differences in development of the terminalia would be apparent only in the earlier nymphal metamorphoses.

Family Listrophoridae Canestrini.

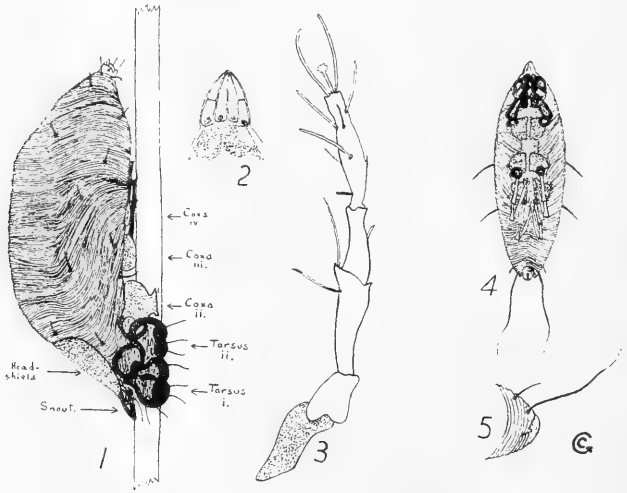
Genus Labidocarpus Trouessart 1895.

Ann. Soc. ent. France, lxiv, Bull., xxxviii.

Labidocarpus bulouensis, n. sp. Figs. 1–5.

Many last-stage nymphs and/or young adults, from a scrub wallaby (a local highland form of *Macropus* (*Thylogale*) *coxeni* Gray 1866), taken at Bulolo, T.N.G., November, 1939.

Body flat or concave ventrally, rounded dorsally, tapering caudally; the male longer and stouter; the female slighter, and curved ventrally from front to rear. The body with pronounced heavy coarse transverse striations. Ventrally, between the coxae, a shallow groove with fine transverse striations. Colour dark chocolate-brown. Female: Length, 292 to 325μ; height, 100 to 115μ; width, 100 to 115μ. Male: Length, 375 to 542μ; height, 111 to 209μ; width, 111 to 209μ. Snout tapering to a thin margin, point rounded; covered dorsally and laterally with a thin translucent hood. Chelicerae sharply pointed, straight or with a slight ventral curvature. Palpi sharply pointed, lying close alongside the chelicerae as in Figure 2. Hood overlapping the snout, its edges lying on the surface of the supporting hair. Head-shield finely pitted; attached at the base, lying back against the forward slope of the body. Legs, 4: i and ii highly modified for gripping the



Figs. 1-5.—*Labidocarpus buloloensis*, n. sp. 1, Male, lateral view; 2, Dorsal view of snout; 3, Leg iv; 4, Ventral view of female; 5, Lateral view of apex of abdomen, female.

supporting hair, compact, and heavily chitinized, so that details cannot be made out; iii and iv with five segments, not used for grasping the supporting hair, but with the last two segments folded forward beneath the abdomen. Coxae finely pitted; coxae ii project down alongside the supporting hair, but apparently do not grasp it. Each coxa terminates in a chitinized ring, those of legs i and ii very large. The second segments of legs i and ii appear to be composed of two more or less parallel chitinized bars, with lighter material between. The tarsi of legs i and ii are thickened, apparently bilobed, bearing a few short nude setae, as in Figures 1 and 4. Legs iii and iv bear a few nude setae, as in Figure 3; tarsi long and slender, bearing two slender claws and a shorter empodium. Body setae nude, tapering to a fine point: in the male, all short, 26 in number, arranged as in Figure 1; in the female they are longer, those at the apex very long (120 to 150μ), 8 in number, arranged as in Figures 4 and 5. Terminalia at the apex of the abdomen, as in Figure 1 (male) and Figures 4 and 5 (female).

Type specimen in the collections of the School of Public Health and Tropical Medicine, University of Sydney.

THE MUSCULATURE OF THE MANDIBULAR AND HYOID ARCHES IN A STING-RAY (*TRIGONORHINA FASCIATA*).

By G. S. Lightoller, M.D., Department of Anatomy, University of Sydney.
(*Communicated by Professor A. N. Burkitt.*)

(Two Text-figures.)

[Read 31st July, 1940.]

Vetter (1874) described systematically and thoroughly the "Kiemen- und Kiefermuskulatur der Fische". The muscles described were, mainly, the branchial constrictor sheets and their homologues in the mandibular and hyoid arches.

The constrictors were called superficial constrictors; their dorsal or ventral position and the arch to which they belonged were mentioned, and any further subdivision was shown by the use of Arabic or Greek letters. Such a name as the second ventral constrictor part b is typical of those in use; it was abbreviated to csvb2.

Ruge (1896), Marion (1905), and subsequent writers have adopted this classification.

In 1939 a resurvey of this musculature was made in elasmobranch sharks (Lightoller, 1939), when greater attention was paid to the structure of a typical branchial arch. The constrictor sheet, forming the branchial interseptum, was subdivided into (*a*) P. branchialis which lay between the branchiae, (*b*) P. inscriptionalis which lay caudal to the branchiae but was, likewise, supported by the branchial rays; often it was attached to the lateral ray by an inscription, (*c*) P. arcuata whose fibres were unsupported and passed, without interruption, from the dorsal to the ventral surface of the body. It lay in the free edge of the interseptum and formed a "gill hood".

Several facts were disclosed by this closer survey. In each arch a levator muscle was displayed lying deep to each constrictor sheet; this was sometimes weak, but was powerfully developed in the first (mandibular), second (hyoid), and the caudal arch. The levator and constrictor musculature of the branchial arches was found to be supplied by occipito-spinal nerves. In *Mustelus antarcticus* no branches from the Xth cranial nerve were seen to enter this musculature. Further, the innervation of the P. arcuata was identified; this was, wholly or partially, by fibres from the nerve of supply to the P.p. branchialis and inscriptionalis of the interseptum caudal to it; i.e. by a prebranchial nerve.

The application of these findings to the musculature of the mandibular and hyoid arches led to a clearer understanding of this and a new conception of that. Homologues of the P.p. branchialis, inscriptionalis and arcuata and of the levator sheet were disclosed in the mandibular arch musculature. The P. arcuata (cs1c) was constant ventrally; dorsally it was infrequent. Both were always supplied by the VIIth cranial nerve, i.e. by the nerve innervating the caudally adjacent constrictor sheet of the second (hyoid) arch.

Moreover, the P. arcuata dorsalis (csd1c) always lay caudal to the spiracle owing to the rostral movement of the external opening of this cleft. In the present paper the musculature of the mandibular and hyoid arches of the sting-ray will be similarly described. The ventral position of the gill clefts in Rays and Skates, the lateral thinning of the branchial basket and its attachment to the propterygium have caused modifications in the basic plan of the branchial musculature. Such modifications are, phylogenetically, unimportant and will not be described: they are indicated in the dioptograms. In describing the muscles the abbreviations csv1a, csv2a, etc.[1], will be bracketed after the name of the muscle—thus defining the homology of the muscle.

I. Superficial Constrictor Musculature.

A. *Of the First (Mandibular) Arch.*

In this Ray P.p. "a", "b" and "c" of the hypothesized first constrictor sheet are present. The modified cartilages which form the jaws have, however, divided the original sheet into three groups: a dorsal (cranio-palatal); an intermediate (palato-Meckelian); and a ventral (inter-Meckelian). The part "b" includes the three groups of fibres; parts "a" and "c" have dorsal and ventral, but no intermediate component.[2] The above conditions seem common to all elasmobranchs.

Dorsal Group: This consists of three separated muscles: The P. prae-orbitalis (csd1a), which will be described with the M. adductor mandibulae; the P. cranio-maxillaris (csd1b′) and the P. nucho-maxillaris (csd1c).

P. cranio-maxillaris (csd1b′): This is well developed and, at its origin, consists of three bands of interwoven fibres, two superficial and one deep. It takes origin from the deep surface of the post-orbital process (Po.O) and the lateral wall of the otic capsule. The origins of this muscle interlace with those of the first and second levators (L1 and L2). Soon after its origin a single muscle belly is formed which constitutes the posterior wall and floor of the orbit. It is inserted into the dorsal surface of the concavity of the palato-quadrate, lateral to the middle line. The muscle is innervated by the oto-spiracular branch of the Vth. A deeply situated band of fibres passes between the insertion of csd1b′ and that of the first levator (L1).

P. nucho-maxillaris (Levator rostri, csd1c): This is well developed, though less so than the depressor rostri (csv1c). It takes origin from the sheath of the dorsal longitudinal musculature, extending from the fibrous sheath of the second levator (L2) to the vertical superficial ridge formed by fused transverse processes. Caudally the fibres are closely interlaced with those of the P. epihyoidea (csd2a). The fibres quickly taper to form a fine tendon at the level of the second levator (L2). From here the long tendon skirts the spiracle, crosses the M. adductor mandibulae—lateral to the orbit—and the root of the pre-orbital process; it ends in the free margin of the rostral region medial to the propterygium. There is a thin tendon sheath. The course of this tendon mirrors that of the M. depressor rostri (csv1c). The innervation is from the VIIth (indicated on the left side of Fig. 1). In the sharks the P. nucho-maxillaris (csd1c) was always inserted into the cartilages of the jaws, though the P. mandibularis (csv1c) frequently ended

[1] This is a slight variation in the order of the letters suggested by Vetter.

[2] The dorsal "a" fibres are not attached to the palato-quadrate, but pass, as in other elasmobranchs, from the skull to the lower jaw without interruption. Strictly speaking, intermediate "a" fibres are included with the dorsal "a" group. See Lightoller, 1939, Pl. i, fig. 1.

upon the surface of the M. adductor mandibulae. In the rays the dorsal, as well as the ventral, muscle has acquired a similar specialized insertion.

Intermediate Group: Two muscles will be described in this group, the P. prae-orbitalis (csd1a) and the P. quadrato-mandibularis (cs1b″). They form a functional unit—the M. adductor mandibulae.

P. prae-orbitalis (csd1a): A small but well developed muscle; it is seen only in the ventral dioptogram. The origin is by a broad, thin, tendinous sheet from the base of the skull, caudo-medial to the nasal capsule. Passing ventro-caudally, the flat muscle belly lies ventral to the P. quadrato-mandibularis; it ends in a laterally compressed tendon which is inserted into the ventral surface of the mandible (Fig. 2).

P. quadrato-mandibularis (cs1b″): The muscle is a complex one. Like that of *Heterodontus* it has no lateral raphe and its dorsal and ventral portions are discrete. The *dorsal fibres* (csd1b″) form three muscle bellies. The caudal belly takes origin from the caudal end of the palato-quadrate; its superficial fibres end by interlacing, at right angles, with those of the intermediate belly or by being attached to the pre-orbital process; its deeper fibres are inserted into the caudal end of the mandible. Some fibres from the caudal end of the mandible, also, are attached to the pre-orbital process (Figs. 1 and 2). The intermediate belly takes origin from the palato-quadrate rostral to the caudal belly. All its fibres end in the pre-orbital process. The rostral belly takes origin from the nasal capsule; all its fibres are inserted into the pre-orbital process.[3]

The ventral fibres (csv1b″) form two muscle bellies; at first sight there appear to be three, owing to the superficial position of the tendon and belly of the P. prae-orbitalis (csd1a). The large lateral belly takes origin from the ventral surface of the mandible rostral to the attachment of the caudal fibres of the P. inter-mandibularis (csv1b′). The insertion is a very extensive one and lies hidden, to some extent, by the P. prae-orbitalis (csd1a). A few fibres end at the angle of the mouth. The remainder are inserted into the ventral surface of the palato-quadrate, extending from an area medial to the angle of the mouth to the lateral free end of the palato-quadrate (Fig. 2).

The medial belly takes origin from the ventral para-median plane of the lower jaw by a long thin tendon which becomes muscular near the angle of the mouth. A few fibres are attached to the angle of the mouth; the remainder join the deep surface of the lateral ventral belly of the M. adductor mandibularae (Fig. 2). The M. quadrato-mandibularis is innervated by the Vth.

Ventral Group: This consists of three muscle sheets. The two rostral ones form the P. intermandibularis (csv1a′ and b′); the caudal muscle is the P. mandibularis (depressor rostri, csv1c).

P. intermandibularis (csv1a′ and b′): These two muscles help to form the diaphragm of the floor of the mouth. The rostral muscle (csv1a′) takes origin from the concave surface of the mandible close to the middle line and for a short distance lateral to this. The fibres pass obliquely towards the middle line, soon become tendinous and interlace freely with each other and with the fibrous sheet which covers the ventral longitudinal musculature.

The caudal muscle (csv1b′) takes origin from the ventral fascia and is inserted into the ventro-lateral surface of Meckel's cartilage.

[3] This muscle is shown, but not labelled in Fig. 1.

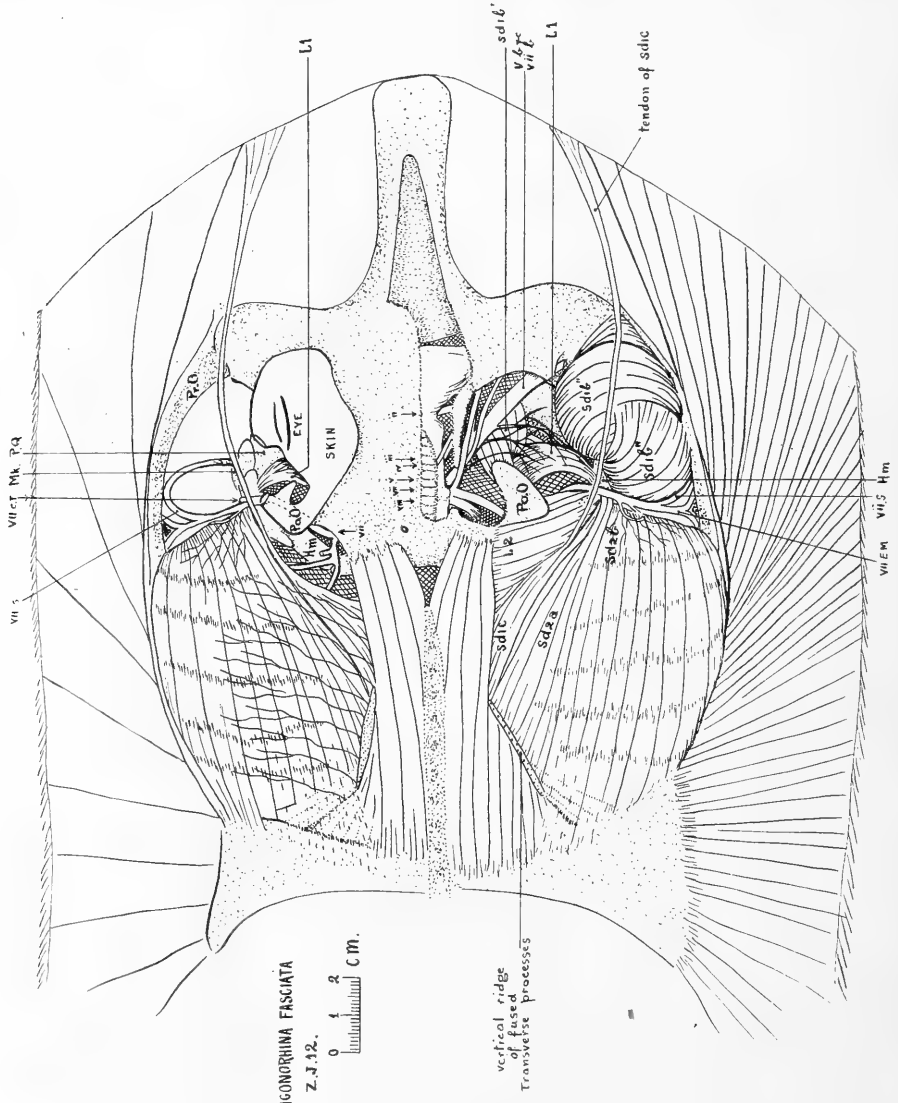


Fig. 1.—*Trigonorhina fasciata*; dorsal view; × $\frac{1}{2}$. On the left side the P. quadrato-mandibularis, the second levator and the lateral wall of the spiracle have been removed. On the right side the eye and its musculature, the dome of the skull and of the otic capsule have been removed. On this side the N.n. otospiracularis and prespiracularis are shown as black lines crossing the orbital cavity.

In both figures the lateral fins have been severed close to the propterygium—though this is not figured. Both figures are dioptograms.

Hm, hyomandibula; *L1*, *L2*, first and second levators; *Mk*, Meckel's cartilage; *Po.O* and *Pr.O.*, post and prae-orbital processes; *P.Q.*, palato-quadrate; *sd1a*, P. prae-orbitalis; *sd1b'*, P. cranio-maxillaris; *sd1b''* and *sv1b''*, P. quadrato-mandibularis; *sd1c* and *sv1c*, levator and depressor rostri; *sd2a*, P. epihyoidea; *sv1a'* and *sv1b'*, P. **intermandibularis**; *sv2a*, P. interhyoidea; *sd2b* and *sv2b*, P.p. inscriptionalis; *sv2c*, P. arcuata ventralis forming the gill hood; *V.b.* and *c*, and *VIIb*, b and c divisions of the Vth and VIIth cranial nerves; *V. Mhy.* mylohyoid branch of the Vth; *VII C.T.*, chorda tympani; *VII E.M.*, external mandibular branch of the VIIth; *VII S*, symphyseal or mandibular branch of the VIIth.

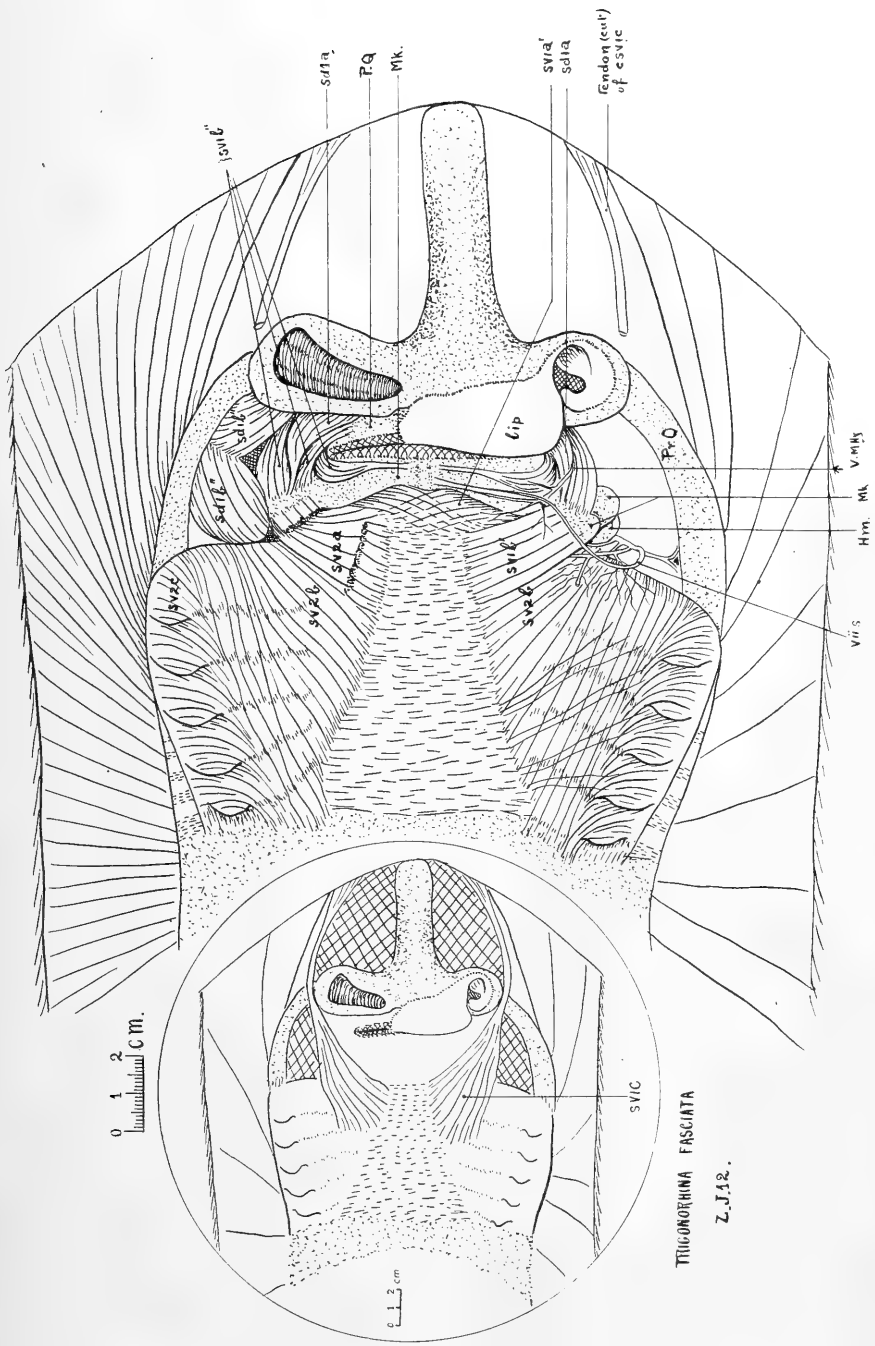


Fig. 2.—*Trigonorhina fasciata*; ventral view, × ½. On both sides the depressor rostri has been removed, but both are shown in the inset (× ¼). On the left side the P. quadrato-mandibularis has been removed. On the right side the upper lip, the covering of the nasal capsule and part of the P. intermandibularis (sv1b′) have been removed. Note the chorda tympani (unlabelled) curling around the neck of the hyomandibula, and the symphyseal branch of the VIIth (VII S) crossing superficial to the mylohyoid branch of the Vth (V.Mhy).

Both these muscles are innervated by the mylohyoid branch of the Vth which lies upon their superficial surface (Fig. 2). The caudal muscle is also supplied by a twig from the VIIth which enters its deep surface (Fig. 2).

P. mandibularis (M. depressor rostri, csv1c) (Fig. 2, inset): This muscle takes no part in supporting the floor of the mouth; it is larger than the M. levator rostri (csd1c). It takes origin chiefly from the fibrous sheet which covers the ventral longitudinal musculature; medially and caudally the fibres are inextricably interlaced with those of the csv1b′, csv2b and branchial musculature. Its fibres converge towards the base of the pre-orbital process passing ventral to the lateral end of Meckel's cartilage and the M. adductor mandibulae. Before reaching the base of the pre-orbital process the muscle fibres are replaced by a stout tendon which runs in a definite sheath. The tendon ends in the free margin of the rostral region medial to the propterygium and immediately ventral to the tendon of the levator rostri (csd1c). A few fibres separate from the muscle belly and form a fine tendon which ends in the angle of the mouth. The muscle is innervated by the VIIth (Fig. 2).

B. *The Superficial Constrictor of the Second (Hyoid) Arch.*

Like the constrictor of a branchial arch, this consists of dorsal and ventral groups; some of the parts into which each of these is subdivided have acquired functional independence.

P. epihyoidea (csd2a): As in *Orectolobus* the muscle is not large enough to cover the second levator (L2). It takes origin from the vertical ridge of the fused transverse processes and from the tendinous aponeurosis separating the second and third arch musculature. Passing rostrally the fibres form a musculo-tendinous sheet which winds around the distal end of the second levator (L2). It gains insertion into the neck of the hyomandibula ventro-lateral to the insertion of the second levator. It is innervated (Fig. 1, left side) by the first extra-cranial branch of the VIIth; this is deeply placed and supplies also the second levator (L2) and the levator rostri (csd1c).

P. interhyoidea (csv2a): As in the sharks, this lies deep to the csv1b′ fibres of the P. intermandibularis. The majority of the fibres take origin from the ventral fascia in common with the fibres of csv1b′, but a few take origin, anterior to this muscle, from the surface of the csv1a musculature. Owing to the poor development of the cerato-hyoid the insertion is unusual. The most superficial fibres pass caudal to the Meckelo-hyomandibular ligament and fuse with the rostral ends of the csd2b and csv2b fibres; some fibres pass deep to this ligament to be inserted into the head of the hyomandibula; the remainder of the fibres are inserted into the cerato-hyoid. The muscle is innervated by the same branch of the VIIth which supplied the csv1b′ fibres of the P. inter-mandibularis.

P. inscriptionalis (csd2b and csv2b): No inscription was seen separating these two muscle sheets; their fibres appear to interlace on the rostral margin of the branchial basket. Both sets of fibres are supplied by the VIIth.

P. arcuata (csd2c[1] and csv2c): The dorsal fibres cover the lateral portion of the branchial basket, but take no part in the formation of the gill hood. This is formed by the csv2c fibres. At the lateral margin of the branchial basket the muscle fibres become fibrous and cannot be traced accurately. The nerve supply of the P. arcuata was not determined.

[1] Not indicated in the dioptogram.

II. Levator Musculature.

First levator (L1): This is a well developed muscle which supports the rostral wall of the spiracle. It takes origin from the lateral surface of the otic capsule where its fibres are interlaced with those of the P. cranio-maxillaris (csd1b′). The fibres are inserted into the lateral end of the hyomandibula (Fig. 1, both sides). It is innervated by the oto-spiracular branch of the Vth.

Second levator (L2)[5]: This is a powerful superficial muscle; it is enclosed in a thin, but strong fibrous compartment which isolates it from the P. epihyoidea (csd2a) and the levator rostri (csd1c). It takes origin, chiefly, from the cartilagincus skull, but some fibres take origin from the fibrous sheath of the dorsal longitudinal musculature. It is inserted into the greater part of the dorsal surface of the hyomandibula, extending almost to the insertion of the P. epihyoidea (csd2a). It is innervated by the first extra-cranial branch of the VIIth—which lies deep to the muscle.

Summary.

A brief account has been given of the musculature of the mandibular and hyoid arches in a ray. Individual muscles have readily been homologized with those found in the elasmobranch sharks. No unfamiliar muscles were found though some were highly specialized. The apparently complete homology of the musculature of the first (mandibular) arch with that of a branchial arch in this ray is in conformity with that recently described by the author for other elasmobranchs.

Acknowledgements.

In conclusion I wish to thank Professor Burkitt of the Department of Anatomy for his continued interest and help; the Department of Anatomy, University of Sydney, for facilities for work and for material; Miss E. C. Pope, Miss M. Hutley, and the Department of Zoology for additional material and the branchial skeleton of a ray.

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[5] Parker and Haswell (*Text Book of Zoology*, ii, 1897, p. 160) figure the skeleton of a sting-ray.

TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XVIII.

THE GENUS OLIGOTOMA WESTWOOD.

By Consett Davis, M.Sc., Lecturer in Biology, New England University College.

(Eighty-three Text-figures.)

[Read 28th August, 1940.]

Genus Oligotoma Westwood 1837.

Trans. Linn. Soc. London, 17, p. 373 (as subgenus of *Embia* Latreille 1829). Raised to generic rank, Burmeister, 1839, *Handbuch der Entomologie*, Bd. II, p. 770. Genotype, *Oligotoma saundersii* Westwood 1837, l.c.

Medium to small Embioptera, the males with the following characters: Winged or wingless; if winged, R_1 usually confluent subterminally with R_{2+3}; R_{4+5}, M, and Cu_{1a} simple; R_{4+5} subobsolescent terminally, M and Cu_{1a} subobsolescent throughout. First segment of hind tarsi elongate, with a ventral bladder terminally, the remainder of the ventral surface clothed with setae. Tenth abdominal tergite cleft longitudinally, division usually subobsolescent anteriorly, sometimes continued to ninth tergite as a groove; hemitergites always in contact basally, not separated by membrane. Right hemitergite with outer margin produced backward and inward to a long process, straight or slightly sinuous, at least four times as long as thick, internal margin basally overlying an obtuse flap, sclerotized only medially. Left hemitergite with a process, simple or complex. First segment of left cercus subcylindrical to strongly clavate, never echinulate; second segment distinct, subcylindrical, at least three times as long as thick. Left cercus-basipodite often complex.

Differentiated from *Navásiella* Davis, *Diradius* Friederichs, and *Oligembia* Davis, by the simplicity of R_{4+5}; from *Teratembia* Krauss by the simplicity of R_{2+3}; from *Anisembia* Krauss and *Mesembia* Ross by the lack of nodules on the first segment of the left cercus; from *Saussurembia* Davis by the presence of an inner process on the right hemitergite; and from *Burmitembia* Cockerell, *Notoligotoma* Davis and *Metoligotoma* Davis, by the altogether different form of the terminalia, especially the left cercus. The above represents a list of only one salient point of difference from each of a number of genera; many other criteria might be selected in each case. Nevertheless, members of several of the above have been wrongly referred to *Oligotoma* at some time (*Oligembia hubbardi* (Hagen), *Navásiella sulcata* (Navás), *Notoligotoma hardyi* (Fried.), *Anisembia texana* (Mel.), *Mesembia hospes* (Myers), *Saussurembia ruficollis* (Sauss.)). In the case of *Mesembia*, *Saussurembia*, *Anisembia* and *Notoligotoma*, this incorrect generic classification has been due to convergence in the venation; in the case of *Navásiella*, no charitable explanation for the confusion with *Oligotoma* can be found.

The possibility of an obscure relationship between *Oligotoma* and *Oligembia* (and possibly other related genera such as *Diradius* and *Teratembia*) has been mentioned earlier (Davis, 1939*b*). In no other case does there seem to be any possibility of true relationship between *Oligotoma* and the above genera, the resemblance being merely superficial (small size, etc.) or convergent (loss of R_5).

The closest relative of *Oligotoma* appears to be the wingless Mediterranean genus *Haploembia* Verhoeff, in which there is agreement, general though not exact, in the form of the terminalia. *Haploembia*, however, has two relatively large hind metatarsal bladders.

Enderlein (1912, p. 72) gives additional generic characters in the process of the ♂ left cercus-basipodite, and the reduced first abdominal sternite of the ♀. In his 'Nachtrag', Enderlein (1912, pp. 108-109) notes that other genera may have a process to the left cercus-basipodite (labelled by him, in the main part of his work, 'ast_9' or Anhang des 9. Sternites). It has been noted (Davis, 1939*c*) that this may include the left half of the larval tenth sternite in some cases; in some species of *Oligotoma* (including the genotype, *O. saundersii*) the true cercus-basipodite appears to have a process, and in addition there is present a latero-ventral process on the left of the hypandrium, which may represent the left half of the larval tenth sternite. In other species, however (e.g. *Oligotoma scottiana* End., *O. gurneyi* Frogg.) the structure appears to be composite (basipodite + tenth sternite), as in most other genera. This character thus fails as a generic criterion.

In all members of the Order studied in both sexes, the first abdominal sternite agrees in the two sexes of one species. In *Oligotoma*, this sternite is rather small (cf. Fig. 11); it is also reduced in all other genera studied by me, often little less so, if at all, than in *Oligotoma*. As might be expected, *Clothoda* has least reduction (Davis 1939*c*). The character seems of little value generically, as no clear line seems to be present, the degree of reduction varying continuously from genus to genus.

The genus *Aposthonia* Krauss 1911 (*Zoologica*, Hft. 60, Bd. 23, p. 48; genotype *A. vosseleri* Krauss 1911, l.c.) is rejected as a synonym of *Oligotoma*. Reasons for this course have been stated previously (Davis, 1936, p. 233). The wings, tarsi and terminalia agree exactly with the present generic description.

Oligotoma saundersii Westwood 1837, *Trans. Linn. Soc. London*, 17, p. 373, and *Oligotoma humbertiana* (de Saussure 1896) = *Embia humbertiana* de Saussure, *Mitt. Schweiz. entom. Gesellschaft*, Bd. 9, Hft. 8, p. 353.—These two species have been dealt with already in this series (Davis, 1939*a*). The synonymy and distribution have been fully discussed, and no further purpose would be served by repeating them here.

Oligotoma nigra Hagen 1885. Fig. 1.

Canad. Entomologist, 17, p. 174.—*Embia nigra* Hagen, 1866, *Verh. zool. bot. Ges. Wien*, 16, p. 221—nom. nud.

Hagen's four cotype males are preserved in the Museum of Comparative Zoology. One is from Cairo, Egypt, coll. Schaum, the other three from Upper Egypt. I have selected the male from Cairo as lectotype, in view of the exactitude of the locality (Rhoda Island, Cairo; cf. Hagen, 1885, p. 175). The other specimens are structurally indistinguishable from the lectotype, which is described below. They are of the same size and colour.

♂ (dry). Length 7·5 mm.; forewing 7·5 × 1·4 mm.; hindwing 6 × 1·4 mm. Colour chestnut-brown, eyes black, wing-veins dark brown, bordered by rather pale-brown bands. Eyes rather large; sides of head behind eyes rounded. Mandibles

as in *O. saundersii*. Wings and tarsi as throughout the genus. Terminalia (Fig. 1) with division of tenth abdominal tergite apparently reaching ninth tergite; outer process of right hemitergite ($10RP_1$) long, smoothly tapered, subobtuse, terminally curved slightly to the right. Inner process ($10RP_2$) normal. Process of left hemitergite (10LP) elongate, simple, tapered, curved slightly to the left, with an oblique line crossing it subterminally. Right cercus with two subcylindrical segments (RC_1, RC_2), basipodite small, subannular. Left cercus with segments (LC_1, LC_2) subequal to right. Hypandrium tapered back to an elongate process (HP), distally truncate, apparently with a tubular membrane (? aedeagus) dorsally; left-hand margin of HP with a subterminal spine (HP_1), sigmoid, terminally acute. Left cercus-basipodite (LCB) separating base of left cercus from hypandrium, flat, produced inward and backward, terminally obtuse, weakly bilobed.

♀. Hagen's two female cotypes, also from Cairo, agree in colour with the males; they seem to be indistinguishable from the females of other species. The lengths are 8 mm. and 9 mm.

Note.—The figure of Enderlein (1912, fig. 59) is obviously from a much-distorted specimen, as noted by Friederichs (1934, p. 415). The latter author (l.c., p. 414 et seq.) gives some interesting bionomical notes on specimens collected at the type locality; he also records the species (♂) from Tel Aviv, Palestine (coll. Bodenheimer).

Synonymy and Distribution.—The species is widespread in Egypt, Palestine and Mesopotamia, often associated with the date-palm. In the British Museum of Natural History are males from the following localities: Cairo, Egypt, coll. W. J. Hall (in alcohol; somewhat paler, therefore, than the dried types). Palestine: Jericho, 28/5/18, E. E. Austin; nr. Jaffa, 2/9/18, E. E. Austin. Arabia: Mecca, 29/1/34, H. St. J. B. Philby. Mesopotamia: Baghdad; Basra; Amara (all coll. P. A. Buxton); Baghdad (coll. H. Scott). The series from Amara has been correctly determined by Silvestri (1923). The specimens from Baghdad collected by Scott represent cotypes of *Oligotoma mesopotamica* Esben-Petersen (1929*a*, *Entom. Mon. Mag.* (3), 15, no. 169, p. 7; nom. nud. by Hugh Scott, foreword on same page). This species is therefore a synonym; the Baghdad series agree with the types in colour, size and detailed structure. The synonymy has been noted by Morton (1929), but denied by Esben-Petersen (1929*b*), who had not seen Hagen's types.

Oligotoma nigra has been introduced into the United States with the date-palm, and is now fairly common in California, Arizona, and adjacent States. Specimens in the Museum of Comparative Zoology include a long series from Tucson, Arizona, collected at light by Dr. F. M. Carpenter, who informs me that the only nest found at the time was in a date-palm. Melander (1903, p. 101) records the presence of Embioptera (incorrectly referred to as *Embia mauritanica* Lucas) on date-palms imported into the United States.

This introduction explains the identity of the species *Embia californica* Banks 1906 (*Trans. Amer. Ent. Soc.*, 32, p. 1; *Oligotoma californica* Banks, 1924, *Bull. Mus. Comp. Zool. Harvard*, 65, no. 16, p. 421[1]). The type (penultimate instar ♂; Los Angeles, California) is in the Museum of Comparative Zoology. It is an *Oligotoma*, but the specific characters (of the mature male) are not developed.

[1] The female figured by Banks (1924, Pl. i, fig. 11) is probably an undescribed species of *Anisembia*; the specimen figured is probably one of a series in the Museum of Comparative Zoology from Niles, nr. San Francisco, California.

The synonymy *E. californica* Banks = *O. nigra* Hagen is further strengthened by a ♂ (Museum of Comparative Zoology) from Mecca, California (date-palm), identified by Banks as '*Embia* ? *californica*'; it is a characteristic specimen of *O. nigra*.

The male described by Hagen (1885, p. 154) as *Oligotoma michaeli* M'Lachlan (from Amballa, Kumaon Himalayas) is in the Museum of Comparative Zoology. The exact identity of *O. michaeli* is doubtful (infra), but Hagen's identification is certainly incorrect. His specimen is structurally indistinguishable from *O. nigra*; it is darker than the Egyptian (type) and Mesopotamian specimens, and slightly larger (length 8·5 mm.), possibly because it is preserved in alcohol; drying sometimes appears to darken a specimen, as the pale intersegmental membranes lose prominence, but it usually renders the sclerite somewhat paler. The record extends the range of *O. nigra* to India with certainty.

OLIGOTOMA GREENIANA Enderlein 1912. Figs. 2-11.

Coll. zool. de Selys-Longchamps, fasc. 3, p. 82, fig. 55.

Enderlein's figure is very confused, showing no process on the left hemitergite, the end of the true process of the left hemitergite being labelled ninth sternite, with no anterior attachment indicated. The species is here re-described from three males and one female, collected by the writer at Colombo, Ceylon. Enderlein's specimens were from Peradeniya, Ceylon, coll. Green. Friederichs (1923, p. 6) has noted the occurrence of this species near Colombo (Mt. Lavinia, etc.), but has not described the male. Two males in the Colombo Museum (Peradeniya, coll. Green, 1910), probably of the series from which Enderlein received the type specimens, agree with the present description of the better-preserved Colombo specimens.

♂. Length 6–7 mm.; head 0·9–1·0 × 0·8 mm.; forewing 4·5–4·8 × 1·2–1·4 mm.; hindwing 3·8–4·0 × 1·2–1·4 mm. (Enderlein's data for the types are: Length 6·5–7 mm.; length of forewing 6 mm., of hindwing 4·5–4·8 mm.). General colour dark chocolate-brown, eyes black, wings with dark-brown veins bordered by mid-brown bands. Head (Fig. 2) broad, with eyes prominent, sides behind eyes rounded. Mandibles as in *O. saundersii*. Wings (Fig. 3) and hind tarsi (Fig. 4) as throughout the genus. Terminalia (Figs. 5–10) complex; outer process of right hemitergite ($10RP_1$) with a terminal dorsal hook (Figs. 6–7), and a flat subacute ventral flange on the left; membraneous inner part of $10RP_1$, basally overlying inner process ($10RP_2$), rather broad. $10RP_2$ normal. Process of left hemitergite (10LP) broad, irregularly tapered, left half of basal portion almost membraneous, not pigmented; termination of 10LP heavily-sclerotized, complex, with a terminal ventral flange on the left, obtusely bifid, and a small subterminal acute spine on the right and above (Fig. 8). Right cercus with two subcylindrical segments (RC_1, RC_2), with a subannular basipodite (RCB). Left cercus with first segment (LC_1) slightly clavate, second (LC_2) subcylindrical. Hypandrium (H) produced backward to an obtuse elongate process (HP), laterally more or less membraneous, medially sclerotized and pigmented; HP with a subterminal lobe on the left, dorsally membraneous, tubular (apparently the aedeagus). Base of left cercus separated from H by a plate-like basipodite (LCB), produced backward as a flat subtriangular lobe. An acute process (HP_1), fused to the left-hand margin of H to the right of LCB, probably represents the left half of the larval tenth sternite; in some other species, the structure classed and labelled as the left cercus-basipodite is probably a composite structure, including as the distal part the process here labelled HP_1.

♀. Length 8 mm., head 0·9 × 0·8 mm. General colour, tarsi, and first abdominal sternite (Fig. 11) as in the male. Apparently indistinguishable from the females of other species of *Oligotoma*.

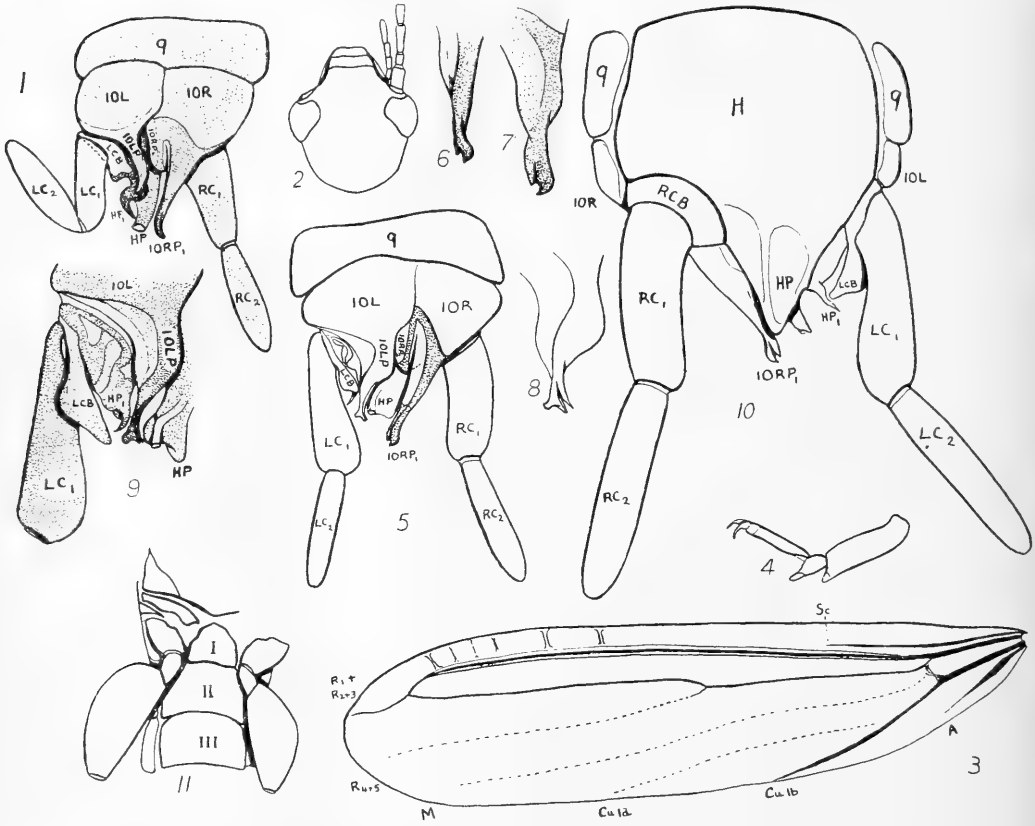


Fig. 1.—*Oligotoma nigra* Hagen, cotype ♂ (lectotype), terminalia from above, × 30.

Figs. 2-10.—*Oligotoma greeniana* Enderlein, ♂ from Colombo. 2. Head from above, × 20. 3. Left forewing, × 20. 4. Hind tarsus viewed laterally, × 40. 5. Terminalia from above, × 40. 6. Outer process of right hemitergite from above, × 60. 7. The same, from above and to the left, × 60. 8. Process of left hemitergite from above, × 60. 9. Base of left cercus and associated structures, viewed from above, × 60. 10. Terminalia from below, × 60.

Fig. 11.—*Oligotoma greeniana* Enderlein, ♀ from Colombo. First abdominal sternite and adjacent structures, × 20 (I, II, III, abdominal sternites).

Setae omitted except in Figs. 13, 18 (wing-fringe), 20, 22, 38 (setae on antennal segments) and 24, 40 (tarsal segments).

All original figures based on camera lucida outlines except 32 and 46-48, which were prepared with constant reference to an ocular micrometer.

Conventional lettering for venation.

9, ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, $10RP_2$, posterior and inner processes of 10R; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; VIII, eighth abdominal sternite; H, hypandrium; HP, main process of hypandrium; HP_1, lateral (left) subterminal process of hypandrium (probably included under LCB in species where it is not labelled as distinct; v. text).

Distribution.—Peradeniya, Ceylon, coll. Green (Enderlein's types, Mus. Stettin; ♂, Colombo Museum); Mt. Lavinia, Ceylon (Friederichs, 1923); Colombo, Ceylon (♂, ♀, in the Macleay Museum, Sydney University; ♂ in the British Museum). Surigao, Mindanao, Philippine Isds. (a male in the Museum of Comparative Zoology, Harvard University, structurally indistinguishable from Ceylon specimens; length 5·5 mm.; head 1·1 × 0·8 mm.; forewing 4·8 × 1·1 mm.; hindwing 4·2 × 1·1 mm.).

Specimens in the Colombo Museum indicate that this species is common and widespread in Ceylon.

OLIGOTOMA WESTWOODI Hagen 1885. Figs. 12–19.

Canad. Entomologist, 17, p. 171 (nom. nud., Hagen, 1866, *Verh. zool. bot. Ges. Wien*, 16, p. 222).

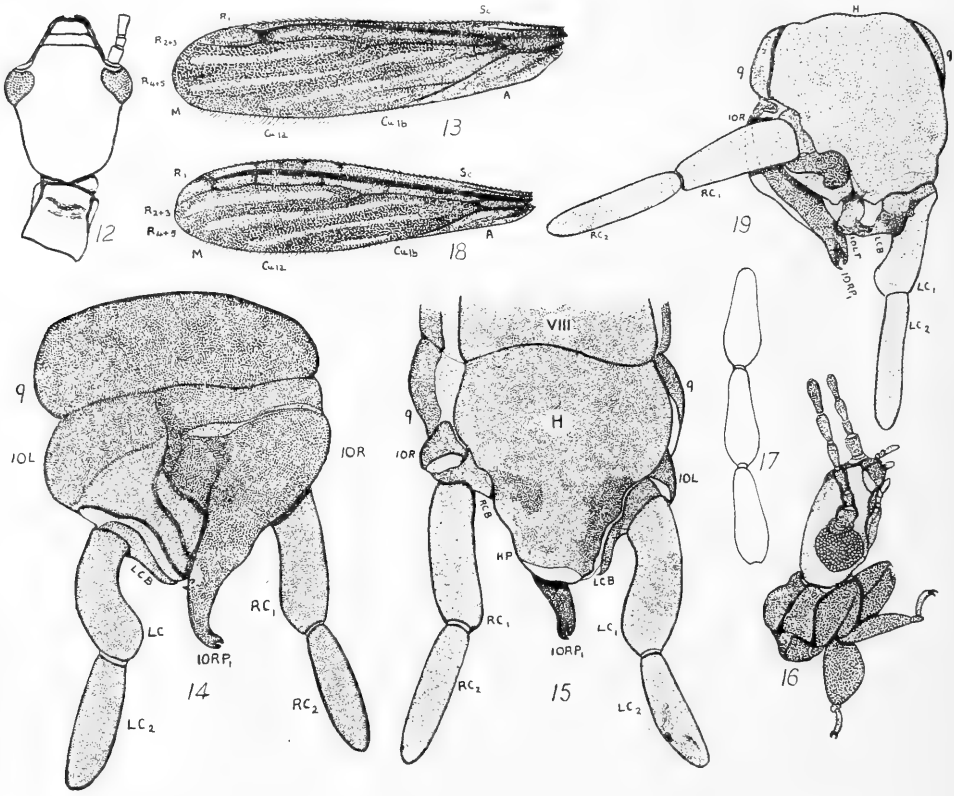
Hagen's two cotypes (♂), in copal (?Zanzibar), are in the Museum of Comparative Zoology. I am much indebted to Dr. F. M. Carpenter, of Harvard University, for assistance in grinding and clearing the cracked copal blocks in which they were embedded.

The two cotypes are apparently conspecific, with minor differences in the wings and antennae, as noted by Hagen (1885, p. 173). In one copal block, there is a Braconid embedded in addition to the *Oligotoma*; in the other, the *Oligotoma* is alone present; the specimens are herein referred to as cotype A (with Braconid) and cotype B respectively.

♂. A: Head 0·7 × 0·55 mm.; length of thorax 1·5 mm., of abdomen 2·1 mm.; total length 4·3 mm. Forewing 3·2 × 0·8 mm.; hindwing 2·5 × 0·8 mm. B: Length of head 0·7 mm., of thorax 1·5 mm., of abdomen 1·3 mm.; total length 3·5 mm.; forewing 3·0 × 0·75 mm.; hindwing 2·5 × 0·75 mm. General colour (by comparison with balsam mounts of recent species) golden-brown, head very dark brown; wings with R_1 and stem of cubitus dark brown, other veins paler, wing-bands pale brown. Head (Figs. 12, 16) with large prominent eyes, sides behind eyes rounded, converging posteriorly. Antennae apparently complete in both cotypes, terminal segment rounded, equal number of segments on left and right; exclusive of the small basal sclerite, there are 15 segments in cotype A, 14 in B; each antenna about 1·5 mm. long. Distalia (Fig. 17) slightly dilated distally. Prothorax with a transverse furrow in anterior third (Figs. 12, 16). Legs as in all recent species of *Oligotoma*. Wings slightly different in the two cotypes; in cotype A, R_1 is connected subterminally by a thick cross-vein to R_{2+3}, and also gives off a twig towards the margin; no other cross-veins present (Fig. 13; all four wings of same structure). In cotype B, more cross-veins are present, somewhat variable in the four wings, some five from R_1 to costa, four from R_1 to sector. Terminalia (Figs. 14, 15, 19) complex; in cotype B, the wings almost wholly obscure the dorsal view, but the ventral view, allowing for a somewhat different arrangement of the various structures due to position at death, agrees well with cotype A. Posterior process of right hemitergite ($10RP_1$) elongate, slightly tapered, distally curved outward slightly, bidentate; outer tooth acute, incurved, inner subacute, straight. Inner process ($10RP_2$) normal in shape; the medial chitinization seen in other members of the genus is not apparent. Process of left hemitergite (10LP) tapered, terminally bent outward and downward as an acute hook. Right cercus with two subcylindrical segments (RC_1, RC_2), the first very slightly clavate, and bent inwards in cotype A. Basipodite (RCB) apparently produced posteriorly, irregularly sclerotized. Left cercus with two subcylindrical segments (LC_1, LC_2), the first slightly incurved and dilated subterminally on the inner side. Hypandrium

(H) tapered posteriorly, obtusely truncate. Left cercus-basipodite (LCB), between H and base of LC_1, acutely tapered, terminally curved outward.

The age of these specimens may be taken as Pleistocene, of the order of half-a-million years old. According to Hagen's data (l.c.), they probably originated from Zanzibar.



Figs. 12-15.—*Oligotoma westwoodi* Hagen, cotype ♂ (A). 12. Head and prothorax from above, × 30. 13. Left forewing, × 16. 14. Terminalia from above, × 64. 15. Terminalia from below, × 64.

Figs. 16-19.—*Oligotoma westwoodi* Hagen, cotype ♂ (B). 16. Head, prothorax and front legs, viewed from right, in front, and slightly above, × 30. 17. Antenna: Three of distalia, × 64. 18. Left forewing, × 16. 19. Terminalia from below, × 64 (more from the right and behind than the view of cotype A in fig. 15).

Oligotoma michaeli M'Lachlan 1877. Figs. 20–21.

J. Linn. Soc. London, Zool., xiii, no. 70, p. 383, Pl. xxi.

The type ♂ (M'Lachlan Collection, British Museum) lacks the terminalia. There seems, therefore, little hope of recognizing the species. Its original locality is not exactly known; it was collected in a London orchid-house in the roots of *Saccolobium retusum*, presumably from India. M'Lachlan's remarks concerning the terminalia would fit many known species of *Oligotoma*, and his figure (l.c., Pl. xxi, 3) is obviously inaccurate; it shows only nine abdominal tergites, the last symmetrical, semicircular and entire.

The following details of the type, which has rather unusual antennae and head-structure, may serve to identify with it more complete specimens collected in the future:

♂. (Length 10·5 mm., after M'Lachlan); head 2·1 × 1·6 mm.; forewing 9 × 2·1 mm.; hindwing 7·5 × 2·1 mm. General colour dark chocolate-brown (M'Lachlan gives 'deep black, somewhat shining'; this probably accounts for his description of *Embia persica*, in the same work, as of this colour, whereas more recently collected series are brown; there seems to be a tendency in some of the early works to describe the colour of dark-brown specimens as black). Wing-veins dark brown, bordered by smoky-brown bands. Head (Fig. 20) elongate; eyes prominent, sides of head behind eyes converging posteriorly. A depression occupies the region posterior to the clypeus; it is subrectangular, opening forward. Left antenna broken; right with 21 segments, also incomplete (M'Lachlan gives 24 segments). The 20th and 21st segments, and the distal half of the 19th, are cream, the rest dark brown. The distalia, except the last few, have very peculiar hairs, length greater than the breadth of the segment, hairs undulating or waved. Wings (Fig. 21) normal for the genus, with some 4 cross-veins each between costa and R_1 and R_1 and sector.

In the M'Lachlan Collection are two immature specimens, almost entirely decayed. They were collected at the same time as the type, but do not help to place the species. It will thus be seen that the identity of *O. michaeli* is unknown, and, probably, will remain so.

Three authors have re-described the species without reference to the type; each handled a different species, and in no case, probably, the same species as M'Lachlan's type. Hagen (1885) described the species from a ♂ of *O. nigra* Hagen, from Amballa (supra); the female he described, thinking it to belong to *O. michaeli*, was *Parembia valida* (Hagen) (= *Embia major* Imms).

Friederichs (1934, p. 415, figs. 5*a-c*) described both sexes from specimens collected at Pahang, Malay States. This description agrees moderately closely with M'Lachlan's type, in size and colour as well as in the structure of the head and antennae. The terminalia seem scarcely distinguishable from *O. ceylonica* Enderlein 1912; Enderlein's description of the head and antennae of this species (1912, p. 83) agree with Friederichs' data. However, a specimen from Ceylon described in this paper (infra), which seems almost certainly to belong to *O. ceylonica*, is not very strongly suggestive of M'Lachlan's type. In any case, the data are insufficient for the rejection of Enderlein's name in favour of *O. michaeli*.

Mukerji (1935, p. 7, fig. 3) described a male (Assam, Shillong, 4900 ft.). Only the terminalia were described, so that there is no means of comparing this specimen with M'Lachlan's type. It would appear from Mukerji's figure that he was dealing with an unnamed species.

The larva which Krauss (1911, p. 36) believed to belong to *O. michaeli* is probably referable to *Parembia*; the locality is Bombay. Krauss's figure (Pl. i, fig. 5B) shows two hind metatarsal bladders, proving that the specimen is not referable to *Oligotoma*.

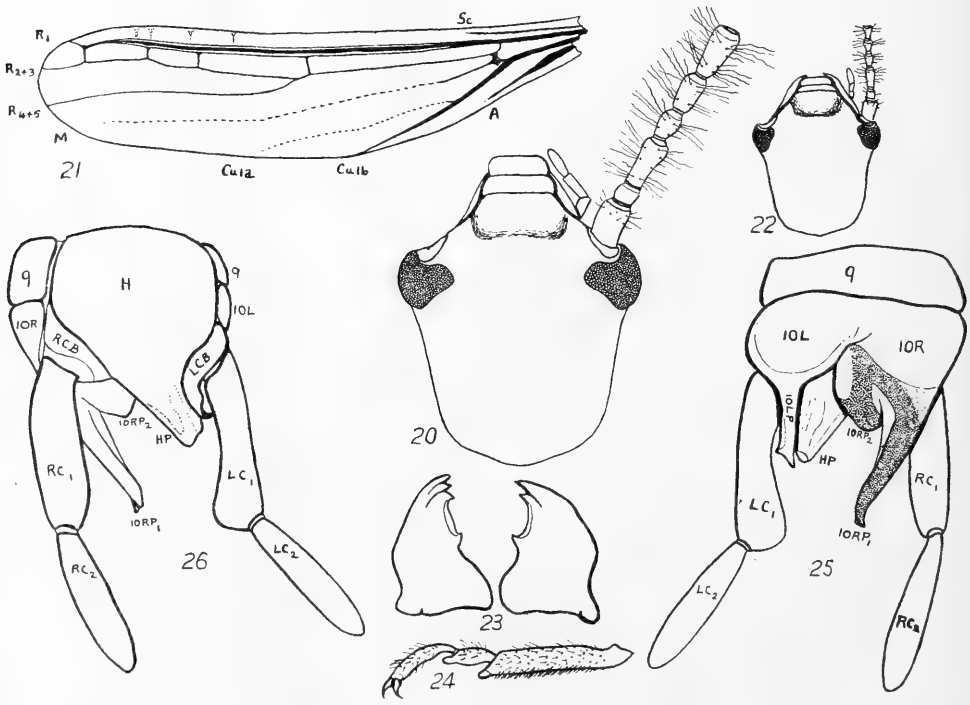
Enderlein (1912, p. 89) referred a female from Java to *O. michaeli* M'Lachlan, erecting a new variety (var. *javana*). The specimen might belong to any species of *Oligotoma* or even, to judge from the description, to *Ptilocerembia roepkei* Friederichs 1923. Enderlein's name, being varietal, need receive no consideration.

OLIGOTOMA THORACICA, n. sp. Figs. 22–26.

Oligotoma collaris Navás, 1928, *Ann. Mus. Civ. Storia Naturale, Genoa*, 53, p. 388.—Not *Haploembia collaris* Navás 1923*a*, *Rev. Acad. Cienc. Zaragoza*, viii, p. 14.

Haploembia collaris was described from a female, from Elisabethville, Belgian Congo; it is probably not a *Haploembia*, and in any case is unrecognizable (Davis, 1939*d*). Two males in the Genoa Museum, from Burma ('Carin Chebà, 900–1100 m(etres), L. Fea, VI.88'), were described as the males of the Elisabethville female, and the species transferred to *Oligotoma* (Navás, 1928). This course was followed on account of a resemblance in coloration.

Colour is a relatively unimportant character in the Embioptera, and many quite unrelated species have the same colour characters as the above specimens (dark brown with orange-brown prothorax). It is a geographic impossibility for the males to belong to the Congo species, to which, unrecognizable though it is, the name *collaris* is rightly limited. Apart from the introduced species (*O. saundersii* Westw.), *Oligotoma* is not known from the Congo, and the males mentioned above cannot belong to a Congo species. They are therefore described as new.



Figs. 20-21.—*Oligotoma michaeli* M'Lachlan, holotype ♂. 20. Head from above, × 20. 21. Left forewing, × 8, somewhat crumpled.

Figs. 22-26.—*Oligotoma thoracica*, n. sp., cotype ♂. 22. Head from above, × 8. 23. Mandibles from above, × 20. 24. Hind tarsus viewed laterally, × 20. 25. Terminalia from above, × 20. 26. Terminalia from below, × 20; process of hypandrium, distad to dotted line, sclerotized only very weakly.

♂. Length 13–15 mm.; head 2·3–2·7 × 1·9–2·1 mm.; forewing 10–11 × 2·3–2·5 mm.; hindwing 8·5 × 2·3–2·5 mm. General colour as in the type of *O. michaeli*, except that the pronotum is orange-brown, and, in the larger of the two specimens, most of the fore-legs also. Head structure (Fig. 22) as in the type of *O. michaeli*; the antennal pubescence also agrees. The smaller specimen has 25 antennal segments, the terminal ones no paler than the rest, the long wavy hairs absent from the last six segments. Navás (1928) gives the number of antennal segments as 31, last segment pale. Mandibles (Fig. 23) with terminal and subterminal teeth directed inward, acute, the left with three, the right two; basad to these is a slight concavity on the inner margin, and a medial tooth, subacute, curving forward. Wings as in *O. michaeli* (cf. Fig. 21), except that the larger specimen has more cross-veins (some 7 from R_1 to sector, and in one wing a trace of one from R_{2+3} to R_{4+5}). Hind tarsi (Fig. 24) normal for the genus. Terminalia (Figs. 25–26) very distinctive; posterior process of right hemitergite ($10RP_1$) elongate, tapered, terminally curved slightly to the right, and truncate, with two weakly-formed teeth, the outer one more dorsal in position; inner process ($10RP_2$) normal. Process of left hemitergite (10LP) straight, distally slightly expanded and obliquely truncate. Right cercus with two elongate subcylindrical segments (RC_1, RC_2), with a small basipodite (RCB). First segment of left cercus (LC_1) elongate, terminally slightly dilated inward; second segment (LC_2) subcylindrical. Hypandrium (H) produced backward to a tapered process (HP), curved slightly to the left, obliquely truncate, terminally membraneous at sides, with a medial membraneous bay. Left cercus-basipodite (LCB) probably composite (supra), fused to left side of H, terminally curved out in an acute hook.

♀ unknown.

The two cotype males are in the Genoa Museum.

This is the largest known species of *Oligotoma*, and is very distinctive in many respects. It has a great structural similarity to the type of *O. michaeli* in the parts preserved in the latter. If this similarity extends to the terminalia, none of the species described by Hagen, Mukerji or Friederichs (supra) as *O. michaeli* can be closely related to that species. The specific identity of *O. michaeli* and *O. thoracica* seems unlikely, in view of the fact that the former has the prothorax concolorous with the rest of the body; although colour is unimportant, it should not be neglected entirely.

Oligotoma borneensis Hagen 1885. Figs. 27–37.

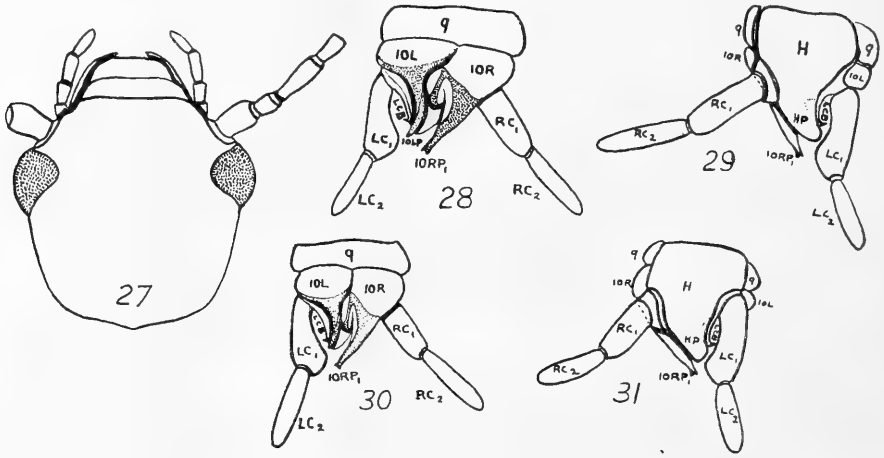
Canadian Entomologist, 17, p. 146.

Hagen (l.c.) re-described *Oligotoma saundersii* Westw. from eight examples (♂) from Borneo. Concerning these, he wrote: 'Their different colour [from previous descriptions of *O. saundersii*—C.D.] induced me to name them as a new species, especially as mine are well preserved in alcohol, and Wood-Mason's, of the same uniform brown colour, were also in alcohol. Thirty years ago I twice studied the type of *E. Latreillii* Ramb. As I do not find my notes, I believe it to be more prudent to unite the Borneo specimens with *O. saundersii*, the more so as Rambur's description agrees'. Krauss (1911) lists *O. borneensis* Hagen under the synonymy of *O. saundersii*.

Hagen's eight specimens are in the Museum of Comparative Zoology, Harvard University, consisting of four males in alcohol, labelled 'Telang, Borneo,—12.81'; 'Hagen'; 'Olig. Borneense Hag.' (sic), in Hagen's writing; three males in alcohol, labelled 'Lambang Hiang, Borneo, Sept. '81. Graborsky'; 'Hagen'; and one pinned

male, presumably Hagen's eighth specimen, labelled 'Duson Timor, Borneo, 1.82'. These eight specimens are all conspecific with the species now known as *Oligotoma vosseleri* (Krauss 1911). They are no relation to *O. saundersii* in any sense. It appears that *O. borneensis* must displace Krauss's name; Hagen's name cannot be classed as a nomen nudum, as the whole of his lengthy re-description of *O. saundersii* refers only to these eight specimens.

The series from Telang, S.E. Borneo, bearing Hagen's label 'Olig. Borneense', may be taken as the type series; the other series agree in size, colour and structure. The type series is described below.



Figs. 27-31.—*Oligotoma borneensis* Hagen, cotype ♂, Telang, Borneo. 27. Head from above, × 27. 28. Terminalia from above, × 27. 29. Terminalia from below, × 27. 30, 31, another ♂ from the same series, figured as in Figs. 28, 29.

♂. Length 7·5–9 mm.; head 1·2–1·5 × 1·0–1·1 mm.; forewing 4·5–6 × 1·3–1·5 mm. General colour uniform mid-brown, head a little darker, eyes black; wing-veins dark brown, bordered by brown bands. Head (Fig. 27) with rather large prominent eyes, sides behind eyes rounded, converging posteriorly. Mandibles with internal terminal and subterminal teeth (left three, right two), basad to which is a cutting edge, a small blunt tooth, and a semicircular concavity. Antennae with up to 18 segments (in one specimen, 15 segments on each side); antennal length some 3·5 times the head-breadth. Wings and tarsi normal for the genus. Terminalia (Figs. 28–31) with tenth abdominal tergite divided into left and right hemitergites (10L, 10R), the suture oblique, proximally obsolescent. 10R with outer process ($10RP_1$) almost straight, terminally carrying two toothlets, the outer one blunter and more dorsal in position. Inner process ($10RP_2$) normal. Process of left hemitergite (10LP) as in *O. nigra*. Right cercus and basipodite normal; first segment of left cercus (LC_1) slightly dilated subterminally on the inner side, dilation somewhat variable (cf. Figs. 28, 30). Second segment (LC_2) subcylindrical. Hypandrium (H) produced back to an obtuse process (HP), curved to the left. Left cercus-basipodite (LCB) probably composite, fused to left-hand margin of H, terminally curved out in an acute hooklet.

♀. Cf. Krauss, 1911, p. 49.

Synonymy and Distribution:

Aposthonia vosseleri Krauss 1911, *Zoologica*, Hft. 60, Bd. 23, p. 48.—*Oligotoma vosseleri* (Krauss 1911), Enderlein, 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 101.—Krauss's figures of the type ♂ (l.c., Pl. ii, figs. 14, 14A-G) agree well with Hagen's type series of *O. borneensis*; the size also agrees, the colour is somewhat paler. Krauss's figures of the first segment of the left cercus (14D, F) show it as somewhat more slender than in the types of *O. borneensis*, but the thickness varies slightly in the two figures (dorsal and ventral view). Minor variations in the degree of dilation of this segment are characteristic of *O. borneensis*.

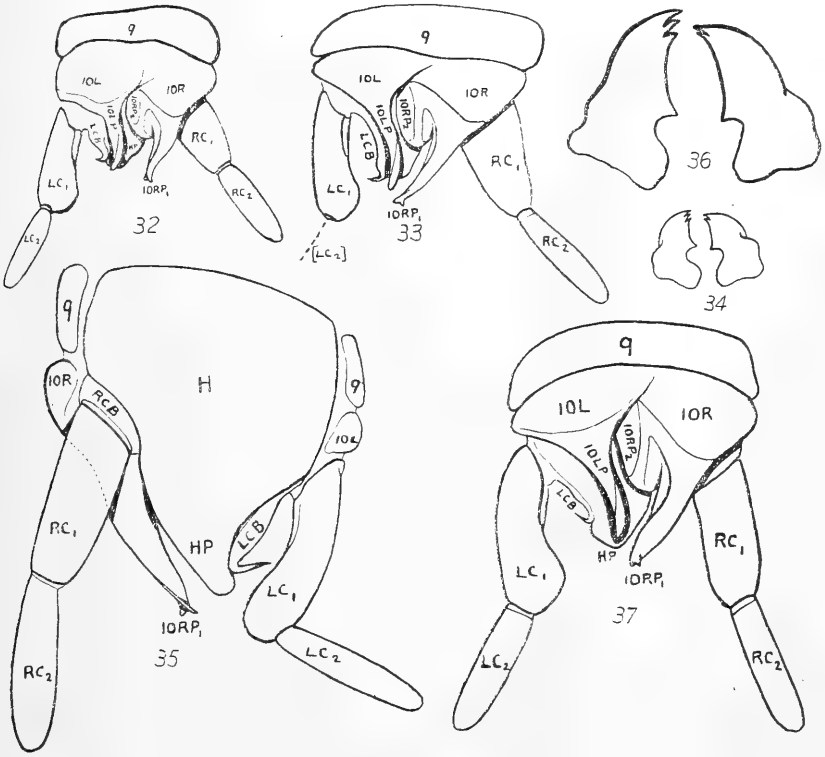


Fig. 32.—*Oligotoma borneensis* Hagen, ♂, from Vigan, Luzon (type of *Oligotoma masi* Navás). Terminalia from above, × 28.

Fig. 33.—*Oligotoma borneensis* Hagen, ♂ from Malaya. Terminalia from above, × 40.

Figs. 34-35.—*Oligotoma borneensis* Hagen, ♂ from Hainan. 34. Mandibles from above, × 20. 35. Terminalia from below, × 60.

Figs. 36-37.—*Oligotoma borneensis* Hagen, ♂ from Tonkin. 36. Mandibles from above, × 40. 37. Terminalia from above, × 40.

Krauss's type ♂ (Mus. Stuttgart) is from Padang, Sumatra; a male from Ceylon (coll. W. Horn; identified by Dr. Friederichs), listed by Krauss (l.c.) under *A. vosseleri*, probably belongs to *O. ceylonica* End. (q.v.), a species which appears to be fairly closely related to *O. borneensis* (infra).

Oligotoma jacobsoni Silvestri 1912, *Tijd. voor Entom.*, 55, p. 334.—The specimen on which this species was based, from Java, is, according to Silvestri's figure, a normal male of *O. borneensis*, the dilation of the first segment of the left cercus being only very slightly different from that in a specimen determined by Silvestri

(l.c.) as *O. vosseleri* (i.e. *O. borneensis*). The colour is apparently darker than in the type of '*O. vosseleri*', agreeing rather with Hagen's series.

Oligotoma maerens Roepke 1919, *Treubia*, i, p. 5.—Allowing for a slight distortion of the segments of the cerci during preparation on a slide-mount, Roepke's figure of the terminalia of this species (l.c., fig. 7) agrees with *O. borneensis* in all respects. It is rather large (length 9·5 mm.; head 1·7 × 1·2 mm.) and dark (Roepke gives: 'Black, with a tinge of dull reddish-violet'). It cannot be considered as structurally distinct from *O. borneensis*, but may be regarded, without name, as a colour-form. The localities are Merbabu, Getassan and Salatiga, Central Java.

Oligotoma nana Roepke 1919, l.c., p. 20.—The specimens described by Roepke differ from the type series of *O. borneensis* only in their small size (length 5 mm.); the colour is described as 'light reddish-grey', probably a different way of describing the normal colour for the paler specimens of *O. borneensis*. The data given for the relative lengths of leg-segments do not serve as a taxonomic criterion; only one (perhaps two) specimens were measured, and the comparison of these measurements with *O. maerens* (i.e. *O. borneensis*) is not significant. Legs regenerating after breakage frequently show such divergence in the relative lengths of the segments. The locality is also Central Java.

Oligotoma masi Navás 1923*b*, *Mem. Pont. Accad. Rom. dei Nuovi Lincei*, Series ii, vol. 6, p. 39.—The type (from Vigan, Luzon, Philippine Isds.; coll. F. Mas, 1919) is recorded as in 'Coll. Navás'. However, in the Paris Museum there is a male labelled 'Oligotoma masi ♂ Nav.; P. Navás S.J. det.'; 'Vigan, Luzon, 1919'; and 'Typus' (Navás' pink type label). It is presumably the type, transferred at some time from the Navás Collection to the Paris Museum. This specimen is a normal example of *O. borneensis* Hagen; the terminalia are illustrated in Fig. 32. The size agrees with Hagen's series (length 7 mm.; forewing 6·5 × 1·8 mm.). The colour (of the dried specimen) is somewhat paler than Hagen's types (in alcohol); it agrees well with dried specimens seen by the writer from Java and Malaya: General colour golden-brown, eyes black, wing-veins dark brown bordered by smoky-brown bands.

Small colour-differences, some perhaps genetic, many undoubtedly concerned with degree of melanization after ecdysis and with method of preservation, cannot be used in this Order as a basis for specific or even racial nomenclature, unless supported by other factors.

Aposthonia vosseleri intermedia Friederichs 1934, *Arch. f. Naturg.*, N.F., Bd. 3, Hft. 3, p. 410.—Friederichs proposed '*intermedia*' as a form, but wrote it as trinomial, the usual annotation of a geographic subspecies. He also reduced *jacobsoni* Silv. and *nana* Roepke to 'forms', but wrote them also as trinomials. *Aposthonia vosseleri intermedia* represents a rather vague colour-difference from the type ('body mid- to dark-brown'), the 'form' *jacobsoni* Silv. being regarded as dark, the type (of Krauss) as lighter. The 'form' *nana* was allowed on size rather than colour.

The recognition of such 'forms' which, as Friederichs (l.c., p. 412) has admitted, do not fit into any regular geographic distribution, does not serve any useful purpose. As noted above, few (if any) are likely to represent genotypic variations, and the time for a genetic examination of the problem is not at hand. In the related species *O. gurneyi*, in a similar case, the subspecific name *O. gurneyi hilli* Davis 1936 has been rejected (Davis, 1938).

Friederichs' localities for the species (regardless of 'form') are: Simalur: Lasikin, Laut Tawar and Sibigo. Sumatra: Padang; Batu; Fort de Kock. Java: Buitenzorg. Malay States: Kuala Lumpur. China: Canton.

Friederichs (l.c., p. 412) also introduced the terminology '*Aposthonia vosseleri obscura*' (under f. *jacobsoni*). In the British Museum is a male from Malaya ('Khumpur'), labelled '♂ *Aposthonia vosseleri* Krauss f. *obscura* = *Oligotoma jacobsoni* Silv.; det. Friederichs 1936'. This specimen was dried, and had not been prepared, indicating that the determination of the form was intended to be based on colour alone, not on structure. The specimen is mid-brown with thoracic nota and back of head paler (ferruginous), a normal coloration for *O. borneensis*. The terminalia are here figured (Fig. 33); in the tip of the outer process of the right hemitergite, and the more excavate base of the first segment of the left cercus, the specimen is intermediate between the typical *O. borneensis* and the Cingalese *O. ceylonica* End. (infra); this might be expected in a Malayan specimen.

Mature males of *O. borneensis* from the following localities have been examined by the writer, in addition to those noted above:

Buitenzorg, Java (Zool. Museum, Buitenzorg): A number of specimens (♂), some determined by Friederichs as *Oligotoma vosseleri*. All agree substantially with Hagen's types, some being a little paler, and with the first segment of the left cercus a little less dilated.

Dwa Bi, Hainan Island (coll. L. Gressitt, 20.7.35; Museum of Comparative Zoology, Harvard University). A series of males, general colour golden-brown, eyes black, wings with dark-brown veins bordered by smoky-brown bands; length 6·5–7·5 mm.; head 1·3–1·6 × 1·1–1·2 mm.; forewing 5–6 × 1·2–1·8 mm.; hindwing 4·5–5 × 1·2–1·8 mm. Mandibles (Fig. 34) and terminalia (Fig. 35) as in Hagen's types, the hooklet at the end of the left cercus-basipodite (LCB) somewhat longer, the first segment of the left cercus (LC_1) a little more slender.

Ta Hian, Hainan Island (coll. L. Gressitt, 13.6.35; Museum of Comparative Zoology). A male agreeing with the above, slightly larger (length 9 mm., head 1·3 × 1·0 mm., forewing 7 × 1·4 mm., hindwing 6 × 1·4 mm.).

Pattam, Tonkin (coll. R. E. Wheeler, 12.29; Museum of Comparative Zoology). Two males, agreeing with the above; length 8–9 mm.; head 1·3–1·4 × 1·1–1·2 mm.; forewing 6–7 × 1·7–1·8 mm.; hindwing 5–6 × 1·7–1·8 mm. Mandibles (Fig. 36) somewhat more slender, terminalia (Fig. 37) well within the present specific concept.

Galog River, Mt. Apo, Mindanao, Philippine Isds., at 6000 ft. (Museum of Comparative Zoology). A specimen (♂) agreeing with Hagen's series, but with the terminal hooklet of the left cercus-basipodite shorter and blunter. In this respect it approaches *O. japonica* Okajima (Japan, Formosa; infra), although a specimen from Luzon (type of *O. masi* Nav.), to the north of Mindanao, fails to show this approach to *O. japonica*. Four males from Los Baños, Philippine Isds. (Museum of Comparative Zoology) also agree with Hagen's type series in all respects.

OLIGOTOMA ALBERTISI Navás 1930. Figs. 38–42.

Brotéria, Série Zoológica, XXVI, fasc. 1, p. 20, fig. 2.

The following re-description is from the unique type ♂ (Mus. Genoa):

♂. Length 9 mm.; head 1·8 × 1·5 mm.; forewing 8 × 2·2 mm.; hindwing 6·5 × 2·0 mm. Colour (dry): Head dark brown, almost black, eyes black, antennae dark brown. Pronotum dark golden-brown, meso- and metascutum dingy yellowish-brown; legs dark brown; abdomen dark brown. Wing-membrane very dark smoky grey-brown, R_1 and cubital stem almost black; inter-venal lines very fine, hyaline. Head (Fig. 38) rather elongate, eyes prominent, sides behind eyes converging slightly posteriorly. Antennae incomplete; structure of mandibles not determined,

the type being unique. It is therefore impossible to be certain whether the basal concavity of the mandibles is present as in the related *O. borneensis* and *O. gurneyi*. Wings (Fig. 39) and hind tarsi (Fig. 40) normal for the genus. Terminalia (Figs. 41–42) showing general similarity to *O. borneensis*, of which this may possibly prove to be a subspecies. The outer process of the right hemitergite ($10RP_1$) has its distal truncate face broader, the two component teeth being less prominent than in *O. borneensis*. The first segment of the left cercus (LC_1) has the internal dilation smoother and less prominent than in *O. borneensis*. The greatest difference lies in the left cercus-basipodite (LCB), which in *O. borneensis* is curved outward terminally as a sharp hook; in *O. albertisi*, it agrees with the East Australian *O. gurneyi gurneyi* Frogg. in being obtusely tapered and scarcely curved outward terminally. *O. albertisi* differs from all subspecies of *O. gurneyi* in the process of the left hemitergite (10LP), which is simply tapered, as in *O. borneensis*; it lacks the terminal hook characteristic of *O. gurneyi*.

♀ unknown.

Locality.—Katau, New Guinea, coll. L. M. D'Albertis, 1875.

OLIGOTOMA JAPONICA Okajima 1926. Figs. 43–45.

J. Coll. Agric. Imp. Univ. Tokyo, 4, p. 414, Pl. xxxii.

This species is apparently very closely related to *O. borneensis*. Winged and wingless forms of the male are known. The dimensions are: Winged ♂, length 6·5–8 mm., head 1·0–1·1 × 0·8 mm., forewing 5·0–5·6 × 1·2–1·4 mm., hindwing 4·0–4·8 × 1·2 mm. Wingless ♂, length 8–9 mm., head 1·3 × 0·8–1·1 mm. ♀, length 10 mm., head 1·3 × 1·0 mm. General colour dark brown. Terminalia (Fig. 43, after Okajima, l.c., Pl. xxxii, fig. 7) agreeing closely with *O. borneensis*, the first segment of the left cercus (LC_1) slightly different in the position and extent of the internal dilation, the left cercus-basipodite (LCB) with no terminal hooklet. In this last respect, *O. japonica* agrees with *O. albertisi*; both are possibly subspecies of *O. borneensis*, and it is interesting to find this character arising at opposite ends of the specific range (Japan, New Guinea), with typical specimens (LCB hooked) in intermediate zones (e.g. Philippine Isds.).

Localities based on mature males (from Okajima, l.c.): Kagoshima Province, Kyushu proper and islands between Kyushu and Loochoo.

A male in the Museum of Comparative Zoology from Urai, Formosa (coll. L. Gressitt, 1.5.32), i.e. from some distance to the south of the former known range, appears to be referable to *O. japonica*. The first segment of the left cercus appears slightly more irregularly dilated, but the specimen actually had this structure somewhat distorted in the course of preparation. The dimensions (length 6·5 mm., head 1·2 × 0·9 mm., forewing 5 × 1·2 mm., hindwing 4 × 1·2 mm.) and colour agree with *O. japonica*, as does the left cercus-basipodite (Fig. 45). The mandibles (Fig. 44) have the basal internal concavity less marked than in the normal *O. borneensis*. Full details of the mandibles are not given by Okajima.

OLIGOTOMA VARIANS Navás 1922. Figs. 46–48.

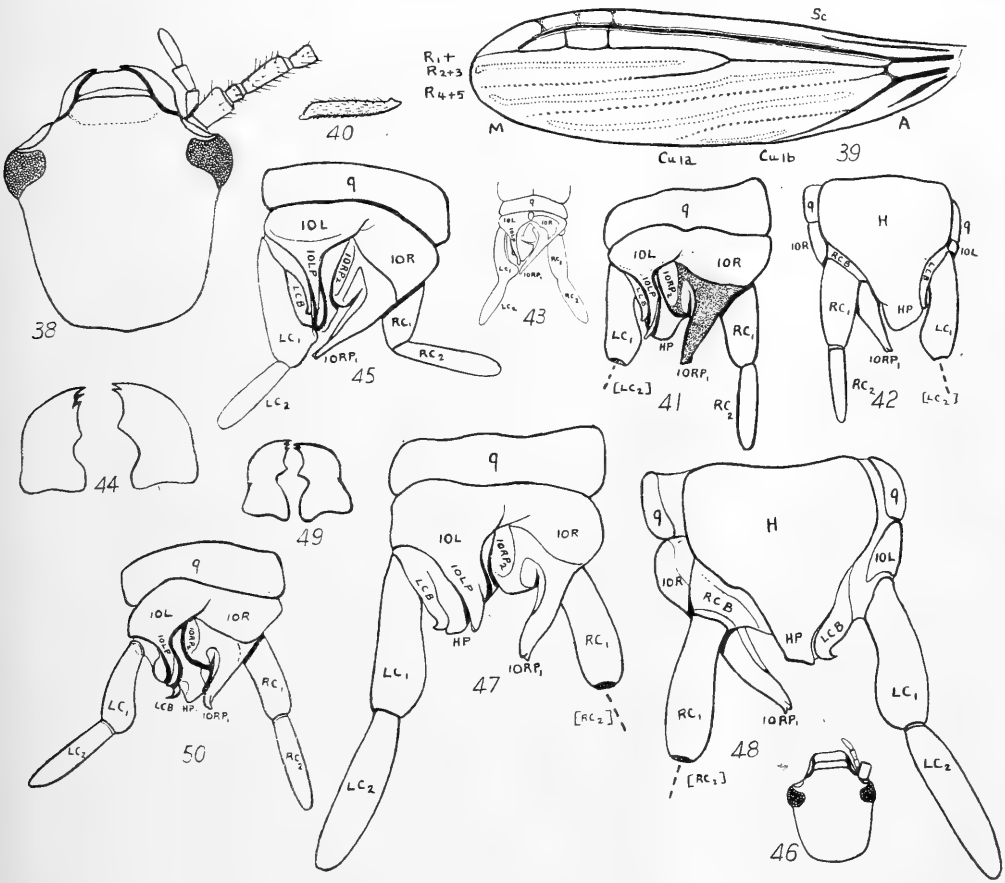
Rev. Acad. Cienc. Zaragoza, vii, p. 32.

The following re-description is from the unique type ♂ (Mus. Paris):

♂. Length 10·5 mm.; head 1·8 × 1·5 mm.; forewings missing, hindwing 7 × 2 mm. General colour dark brown, almost black, wing-veins dark brown bordered by dark smoky-brown bands. Head (Fig. 46) rather elongate, sides converging slightly posteriorly. Venation and tarsi normal for the genus. Terminalia (Figs. 47–48) agreeing rather closely with *O. borneensis*, outer process

of right hemitergite ($10RP_1$) broader, left cercus-basipodite (LCB) rather thick, terminal hook shorter and broader than in *O. borneensis*, whole structure weakly sigmoid. Process of left hemitergite (10LP) very broad; further collecting may prove this to be teratological or individual. 10LP obtusely tapered, with a longitudinal groove on the inner margin. First segment of left cercus (LC_1) scarcely dilated distally. $10RP_2$ rather obtuse.

♀ unknown. (The data given by Navás, l.c., refer to a female from the same locality, but probably not conspecific. It is also in the Paris Museum. The



Figs. 38-42.—*Oligotoma albertisi* Navás, holotype ♂. 38. Head from above, × 20. 39. Left forewing, × 8, inter-venal lines enclosed by dotted lines. 40. First segment of hind tarsus, viewed laterally, × 20. 41. Terminalia from above, × 20. 42. Terminalia from below, × 20.

Fig. 43.—*Oligotoma japonica* Okajima, ♂, terminalia from above, magnification not stated exactly. (After Okajima, 1926, Pl. xxxii, fig. 7.)

Figs. 44-45.—*Oligotoma japonica* Okajima, ♂, from Formosa. 44. Mandibles from above, × 40. 45. Terminalia from above, × 40.

Figs. 46-48.—*Oligotoma varians* Navás, holotype ♂. 46. Head from above, × 8. 47. Terminalia from above, × 28. 48. Terminalia from below, × 28.

Figs. 49-50.—*Oligotoma ? varians* Navás, ♂ from Kwantung. 49. Mandibles from above, × 20. 50. Terminalia from above, × 20.

pronotum is a bright orange-brown; in *O. varians* ♂ it is concolorous with the rest of the body).

Locality.—Gan Chouen Fou, Anshunfu, China, coll. P. Cavalerie, 1912.

This species may later prove to be distinct only subspecifically from *O. borneensis*. Preparation of the unique type to reveal the structure of the mandibles was considered inadvisable.

A male in the Museum of Comparative Zoology, Harvard University, from Yim Na San, East Kwantung, South China, seems to be referable to *O. varians* or to an intermediate between it and *O. borneensis*; the latter would suggest subspecific status for *O. varians*. The colour and dimensions (length 10 mm.; head 1·4 × 1·1 mm.; forewing 7·5 × 1·6 mm.; hindwing 6·5 × 1·6 mm.) agree with *O. varians*. The mandibles (Fig. 49) resemble *O. borneensis*, with a less marked basal concavity internally. The terminalia (Fig. 50) appear to be intermediate in the breadth of $10RP_1$ and the dilation of LC_1; the left cercus-basipodite (LCB) resembles *O. varians*, but is even more markedly sigmoid. The process of the left hemitergite (10LP) is normal for *O. borneensis*, suggesting malformation of this structure in the type of *O. varians*.

Oligotoma ceylonica ceylonica Enderlein 1912. Figs. 51–61.

Oligotoma ceylonica Enderlein 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 83, fig. 56.

This species was described by Enderlein from males taken at Peradeniya, Ceylon. The types are recorded as in the Stettin Museum. Enderlein (l.c.) gave a crude line-figure. Mukerji (1935, p. 4) described males from the type locality (Peradeniya) and from Eastern India (Barkuda Island, Chilka Lake), introducing the new varietal name *O. ceylonica* var. *variegata* for both series. It would appear that the differences noted by Mukerji between his Peradeniya specimens and Enderlein's description are concerned with his more careful study (or Enderlein's lack of detail) rather than with actual structural difference. The Barkuda Island specimens are, likewise, scarcely distinct. Other very different specimens have since been classed under Mukerji's varietal name (Menon and George, 1936; infra).

Enderlein's data may be summarized as follows:

♂. Length 5·5–6·5 mm.; length of head 1·1 mm.; forewing 5·0–5·3 mm., hindwing 4·0–4·2 mm., in length. Colour dark red-brown, head ferruginous. Wings brown, with narrow hyaline inter-venal lines. Head rather small; eyes large, sides of head behind eyes weakly convex. Antennae with 15–17 segments, with long perpendicular hairs. Terminalia (Fig. 51, after Enderlein, l.c., fig. 56) similar to *O. borneensis*; termination of outer process of right hemitergite ($10RP_1$) as in the Malayan example of that species noted above (Fig. 33), the outer toothlet a little less distal in position. No hook-like termination is shown for the left cercus-basipodite, such as characterizes *O. borneensis*.

Mukerji's more careful figures also omit details of the left cercus-basipodite. In other respects (Fig. 52, after Mukerji, l.c., fig. 2*f*) it would appear that the structure, e.g. of the processes of the hemitergites, agrees fairly closely with Hagen's series of *O. borneensis*. However, the first segment of the left cercus (LC_1) is strongly excavate in the basal three-quarters. Minor differences in this structure, and in the tip of $10RP_1$, between the Peradeniya (Figs. 53–54) and Barkuda Island (Figs. 55–56) specimens, are illustrated (after Mukerji, l.c., figs. 2*j-k*, *g-h*).

A male in the Colombo Museum (Mihintale, Ceylon, 7–9.vii.27) seems to be clearly referable to *O. ceylonica ceylonica*: Length 6·5 mm.; head 1·9 × 1·6 mm.; forewing 5·0 × 1·1 mm.; hindwing 4·0 × 1·1 mm. General colour as in the type.

Head and mandibles (Fig. 57) as in *O. borneensis*, the internal concavity of the mandibles less marked. Wings and tarsi as throughout the genus. Terminalia (Figs. 58–61) as in Mukerji's description (supra), the basal excavation of LC_1 less marked, the tip of 10LP and $10RP_1$ slightly different in shape. The region of the left cercus-basipodite differs clearly from *O. borneensis* and related species; a membraneous slit runs obliquely forward into the left-hand side of the hypandrium; on the proximal side of this slit, the outer part of the hypandrium is divided off by a weak suture; this sclerite so cut off probably represents part of a composite left cercus-basipodite. The remainder of the basipodite is represented by a membraneous area between this sclerite and the base of the left cercus, the membrane bearing several small discontinuous sclerotizations.

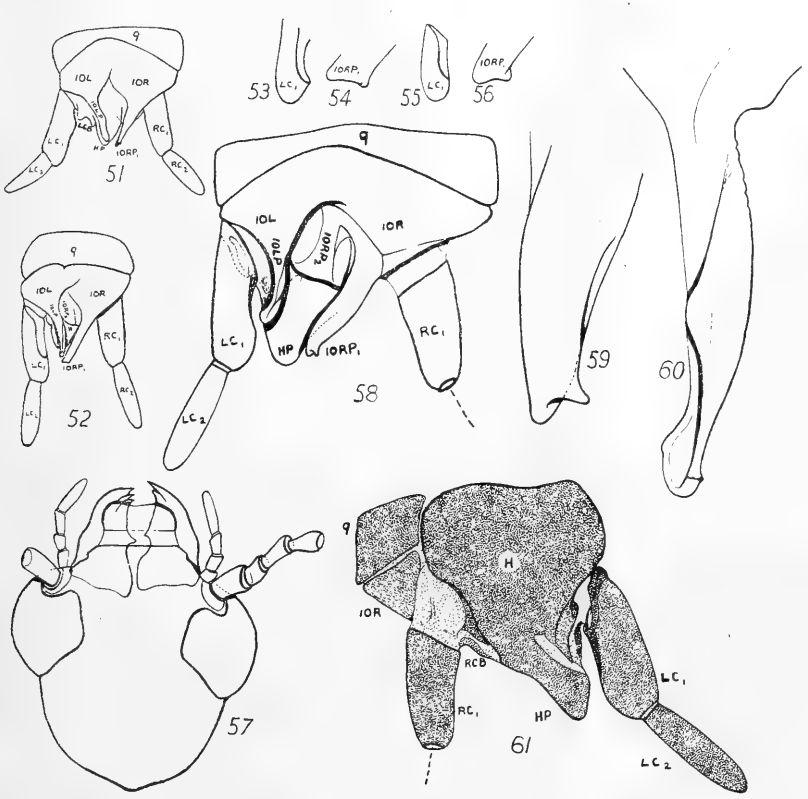


Fig. 51.—*Oligotoma ceylonica ceylonica* Enderlein, ♂, terminalia from above, × 25. (After Enderlein, 1912, fig. 56; type, from Peradeniya, Ceylon.)

Figs. 52-56.—*Oligotoma ceylonica ceylonica* Enderlein, ♂. 52. Terminalia from above, × 12. 53, 54, specimen from Peradeniya, Ceylon. 53. First segment of left cercus from above, × 12. 54. Tip of outer process of right hemitergite from above, × 38. 55, 56, specimen from Barkuda Island, East India: structures and magnifications as in 53, 54. (After Mukerji, 1935, fig. 2, *f*, *j*, *k*, *g* and *h* respectively.)

Figs. 57-61.—*Oligotoma ceylonica ceylonica* Enderlein, ♂ from Mihintale, Ceylon (Colombo Museum). 57. Head from above, × 20. 58. Terminalia from above, × 60. 59. Posterior process of right hemitergite, viewed from above, × 360. 60. Process of left hemitergite from above, × 360. 61. Terminalia from below, × 60.

The absence of the outcurved spine on the left cercus-basipodite is the more remarkable considering its presence in *O. scottiana* End. (Seychelles; infra), the representative of this series from a more westerly locality.

Oligotoma minuta Mukerji 1935 (*Rec. Ind. Mus.*, xxxvii, p. 1), from Calcutta, appears to be a small form of *O. ceylonica ceylonica* End., not specifically distinct. Corresponding forms (without justification for nomenclature) occur in *O. borneensis* Hagen (*'O. nana* Roepke 1919') and *O. gurneyi gurneyi* Frogg. (*'O. gurneyi hilli* Davis 1936').

Oligotoma ceylonica indica, n. subsp. Figs. 62–66.

Oligotoma ceylonica Enderlein, var. *variegata* Mukerji, Menon and George, 1936, p. 92 (Bombay series).

In a very interesting paper, Menon and George (l.c.) referred certain specimens from Cochin (Southern India) and Bombay to *O. ceylonica* var. *variegata*. The Bombay forms are more distinct from *O. ceylonica* End. than is the case for many differences considered as specific in the genus *Oligotoma*; the Cochin forms are intermediate, indicating subspecific rather than specific status for the Bombay specimens.

O. ceylonica seems, therefore, to undergo little change from Ceylon northwards along the East Coast of India, but changes rather remarkably proceeding north-west.

♂ (after Menon and George, l.c.): Length 5–7 mm. Colour as in the type subspecies. Terminalia (Figs. 62–66) immediately differentiated from the type subspecies by the beak-like prolongation of the internal margin of the first segment of the left cercus (LC_1). ♀ unknown.

Locality.—Bombay Presidency: Santa Cruz, Salsette Island; 6 ♂, recorded as in the Bombay University Collection.

The intermediate forms, from Ernakulam, Cochin State, have the first segment of the left cercus less markedly beaked (Figs. 67–69, after Menon and George, l.c.).

Details of the left cercus-basipodite are not given for either the Bombay (type) or Cochin (intermediate) series. The structure is probably inconspicuous, as in the type subspecies.

Oligotoma scottiana Enderlein 1910. Figs. 70–72.

Trans. Linn. Soc. London, Zool., xiv, p. 55.

The following description is from one of Enderlein's cotypes (♂) in the British Museum of Natural History. It may be regarded as the lectotype.

♂. Length 8 mm.; forewing 6·5 × 1·6 mm.; hindwing 5·0 × 1·4 mm. General colour dark brown. Eyes large, sides of head behind eyes converging posteriorly. Wings (Fig. 70) and tarsi normal for the genus, except that R_1 is not confluent with R_{2+3}. Terminalia (Figs. 71, 72) generally similar to *O. borneensis*; outer process of right hemitergite ($10RP_1$) subobtuse, outer tooth situated well before apex. Process of left hemitergite (10LP) broader than in *O. borneensis*, but otherwise similar. First segment of left cercus (LC_1) dilated subterminally on the inner side. Left cercus-basipodite (LCB) as in *O. borneensis*. Hypandrium (H) truncate, right-hand margin terminally represented by a subobtuse tooth, left-hand margin only weakly sclerotized terminally.

Locality.—Mahé, Seychelles, Percy Sladen Trust Expedition.

(Enderlein (l.c.) gives as an additional locality the Cargados Garajos Group. This record is not based on mature males, and has no significance. The presence of *O. scottiana* on Mahé argues for a continental origin, which cannot be extended

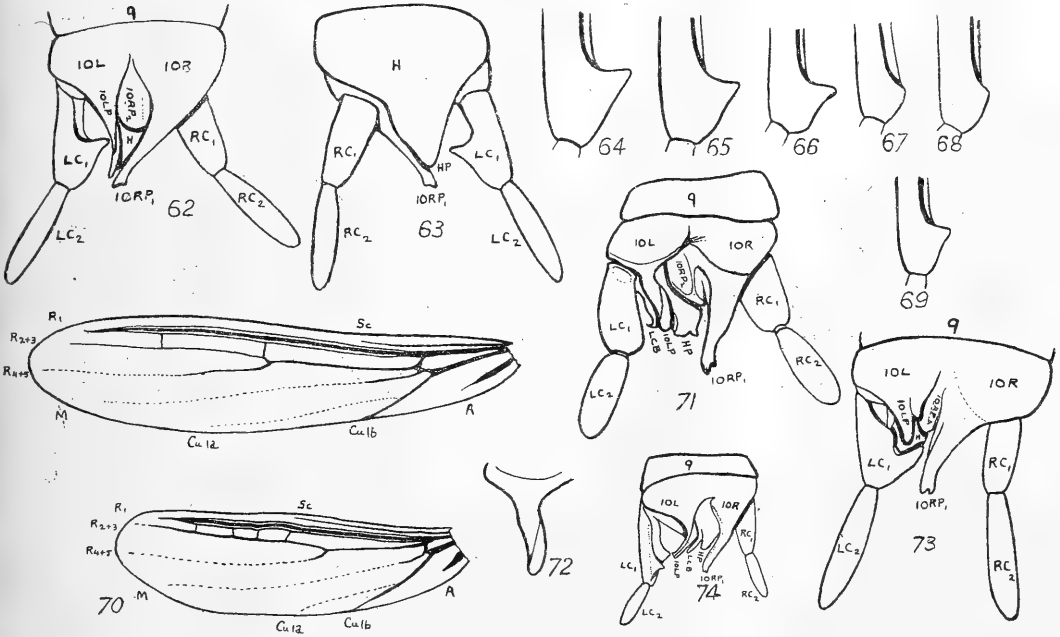
to Cargados Garajos. The specimen from the latter locality probably represents a female of the tropicopolitan *O. saundersii* Westw., spread by man; Enderlein (l.c.) records this species (under the name *O. latreillei* (Ramb.)) from Aldabra Island.)

O. scottiana differs from other species (e.g. *O. borneensis*) by less, probably, than *O. ceylonica indica* differs from *O. ceylonica ceylonica*. Its insular position and isolation suggest that it should be retained as a species rather than reduced to a subspecies of the Eastern series (*O. borneensis*; this latter is probably specifically distinct from *O. ceylonica*, but may include as subspecies *O. varians*, *O. japonica* and *O. albertisi*). A final pronouncement on these questions cannot be given on the available data.

Oligotoma asymmetrica Menon and George 1936. Fig. 73.

J. Bombay Univ., 4, pt. 5, p. 92, Pl. iii.

♂ (after Menon and George, l.c.): Length 9·3 mm.; head 1·5 × 1·2 mm.; forewing 5·5 mm. in length. General colour dark brown (head and prothorax almost



Figs. 62-66.—*Oligotoma ceylonica indica*, n. subsp., ♂. 62. Terminalia from above, × 42. 63. Terminalia from below, × 42. 64-66, variation in first segment of left cercus, × circa 52. (Specimens from Salsette Island, Bombay Presidency, herein named type series. After Menon and George, 1936, Pl. ii, figs. 2*a*, 2*b*, 1*d-f* respectively.)

Figs. 67-69.—*Oligotoma ceylonica*, intermediates between subspecies *ceylonica* End. and *indica*, n. subsp.; ♂ from Ernakulam, Cochin, South India. Variations in first segment of left cercus, × circa 52. (After Menon and George, 1936, Pl. ii, figs. 1*a-c*.)

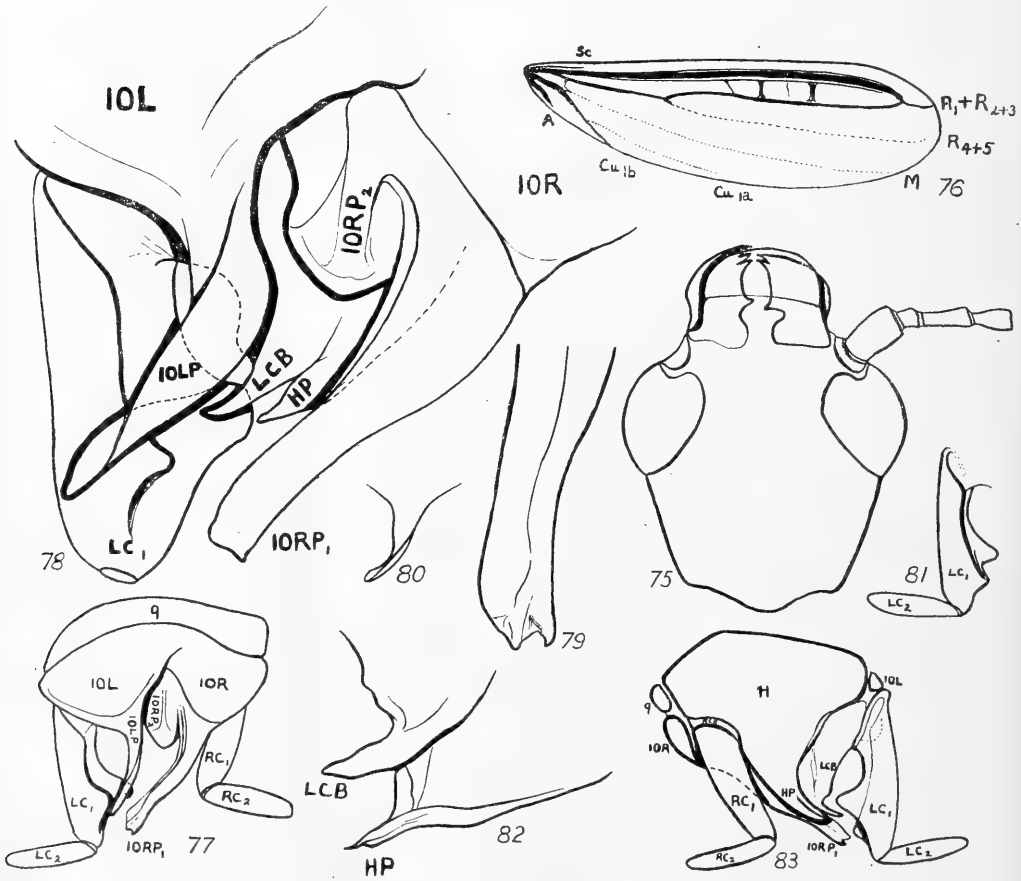
Figs. 70-72.—*Oligotoma scottiana* Enderlein, cotype ♂ (lectotype). 70. Left fore- and hindwing, × 10. 71. Terminalia from above, × 25. 72. Process of left hemitergite from above, × 25.

Fig. 73.—*Oligotoma asymmetrica* Menon et George, ♂. Terminalia from above, × circa 25. (After Menon and George, 1936, Pl. iii, fig. 1.)

Fig. 74.—*Oligotoma minuscula* Enderlein, ♂. Terminalia from above, × 14. (After Enderlein, 1912, fig. 61; from the type, from Daressalam, East Africa.)

black, remainder somewhat lighter). Wings greyish-black, veins brownish-black, inter-venal lines hyaline, distinct. Head rounded; details of mandibles not given. Antennae with 23 segments. Wings normal for the genus. Terminalia (Fig. 73, after Menon and George, l.c., Pl. iii, fig. 1) very distinctive; outer process of right hemitergite ($10RP_1$) rather broad, terminally truncate and weakly bidentate; inner process ($10RP_2$) normal. Process of left hemitergite (10LP) short and obtuse, with a small basal lobe on the right (possibly teratological; cf. the type of *O. varians*). First segment of left cercus (LC_1) remarkable, inner margin produced inwards to two lobes, basal lobe short, subterminal lobe long, slender, curved forward. Hypandrium subtriangular, distally slightly swollen, and concave dorsally; details of left cercus-basipodite not given.

♀ unknown.



Figs. 75-83.—*Oligotoma minuscula* Enderlein, ♂ from Colombo, Ceylon. 75. Head from above, × 60. 76. Right hindwing, × 20. 77. Terminalia from above, × 60. 78. Distal parts of same, exclusive of right cercus and second segment of left cercus, × 180. (Posterior process of right hemitergite distorted terminally.) 79. Posterior process of right hemitergite from above, × 180. 80. Process of left hemitergite from above, × 60. 81. Left cercus from above, × 60. 82. Distal parts of left cercus-basipodite and hypandrium from above, × 180. 83. Terminalia from below, × 60.

Locality.—Bombay Presidency: Santa Cruz, Salsette Island (type presumably in the Bombay University Collection).

OLIGOTOMA MINUSCULA Enderlein 1912. Figs. 74–83.

Coll. zool. de Selys-Longchamps, fasc. 3, p. 87, fig. 61.

♂ (after Enderlein, l.c.). Length 5 mm.; head 1·0 × 0·6 mm.; forewing 3·8 × 1 mm.; hindwing 3·2 mm. × a little less than 1 mm. General colour pale brownish-yellow, wings pale brown, inter-venal lines fine, hyaline. Eyes large; sides of head behind eyes converging strongly posteriorly. Wings normal for the genus. Terminalia (Fig. 74, after Enderlein, l.c., fig. 61) with outer process of right hemitergite ($10RP_1$) curved outward slightly terminally, truncate, with two terminal teeth, the outer one subacute. Process of left hemitergite (10LP) curved to the left, truncate, with a longitudinal groove. First segment of left cercus (LC_1) grooved longitudinally on inner side, each side of the groove (dorsal and ventral) produced in third quarter to an internal angular tooth or lobe.

♀ unknown.

Locality.—Daressalam, East Africa (type in Berlin Zool. Museum).

The discovery of three males in the Colombo Museum (Colombo, Ceylon, coll. 27.11.24, —.9.27 and 26.2.29) enables a fuller description and raises the question whether Daressalam, or Colombo, or both, is the true locality, i.e. whether the record for one of the localities depends on spreading of the species by human transport. Apart from the doubtful *O. westwoodi* Hagen (recorded as probably from Zanzibar; supra), and the pantropic species *O. saundersii* and *O. humbertiana*, the only records of the genus for Africa pertain to *O. nigra*, which may have been spread from Asia (possibly in very early times) by man, e.g. with the cultivation of the date-palm.

Details of the Colombo specimens of *O. minuscula* are:

♂. Length 3·7–4·6 mm.; head 0·7–1·0 × 0·5–0·8 mm.; forewing 3·0–3·6 × 0·9–1·1 mm.; hindwing 2·6–3·0 × 0·9–1·1 mm. Colour as in the type. Head and mandibles (Fig. 75) much as in *O. borneensis*, the head somewhat narrower, with the hind margins more incised laterally. Length of antennae 1·6 mm., with 15 segments on each side. Wings (Fig. 76) normal for the genus. Terminalia (Figs. 77–83) agreeing substantially with Enderlein's description and figure; additional details may be given for the left cercus-basipodite (LCB) (similar to *O. borneensis*, but with the terminal spine broad, subobtuse), and the process of the hypandrium (HP), produced backwards and to the left as a tapered spine. The tip of the process of the left hemitergite (10LP) seems to be smoothly rounded, not truncate.

Australian Species.

Oligotoma glauerti Tillyard 1923, *J. Proc. Roy. Soc. W. Australia*, ix, i; Davis, 1936, p. 242, figs. 6, 13, 20, 27 and 34.

Oligotoma tillyardi Davis 1936, PROC. LINN. SOC. N.S.W., lxi, 5–6, p. 241, figs. 5, 12, 19, 26 and 33.

Oligotoma approximans Davis 1938, PROC. LINN. SOC. N.S.W., lxiii, 3–4, p. 252, figs. 116–119.

Oligotoma gurneyi gurneyi Froggatt 1904, PROC. LINN. SOC. N.S.W., xxix, p. 672.—Davis, 1936, l.c., p. 231, figs. 1, 11, 18, 25 and 32.—Davis, 1938, l.c., p. 252.

Oligotoma gurneyi centralis Davis 1936, l.c., p. 237, fig. 2.

Oligotoma gurneyi spinulosa Davis 1936, l.c., p. 239, fig. 3.

Oligotoma gurneyi subclavata Davis 1936, l.c., p. 240, fig. 4.

Oligotoma gurneyi Frogg., intermediates between subspecies.—Davis, 1936, l.c., p. 239; Davis, 1938, l.c., p. 254; Davis, 1940, Proc. Linn. Soc. N.S.W., lxv, 1–2, p. 158.

The above species and subspecies have been described and figured already in these Proceedings; a repetition of the data seems unnecssary, as the earlier descriptions are in conformity with the descriptions of other species in the present series.

Unrecognizable Species.

Oligotoma ? termitophila Wasmann 1904, Jägerskiöld Exp., No. 13, p. 17; Enderlein, 1912, p. 90.—This species, described from a female from the Sudan, is absolutely unrecognizable; it may belong to one of the tropicopolitan species of *Oligotoma*, or to some other genus. It should be deleted from future lists.

Oligotoma bicingillata Enderlein 1909, *Zool. Anz.*, 35, p. 191.—This name is founded on a female from Pará, Brazil. It is unrecognizable. It may belong to *O. saundersii* Westw. (known to occur in Brazil), or to one of the endemic Neotropical genera.

Oligotoma dichroa Navás 1921, *Rev. Acad. Cienc. Zaragoza*, vi, p. 78.—The type (♂), from Tonkin ('Non loin de la frontière d'Annam, cercle de Ninh binh, an S.S.E. de Hanoi'), is recorded as in the Navás Collection. The terminalia are not described. It would appear from the description that R_{4+5} is forked in the hindwing; this would be unique for *Oligotoma*. The colour and antennae seem to agree with *O. thoracica*, n. sp.; Navás handled the types of the latter without noting any relationship to *O. dichroa*, so that the description of *O. thoracica* as a new species seems justified on the data to hand. *O. dichroa* may be established by a re-examination of the type, if it is still extant.

Discussion.

Taking the Indo-Malayan region as the original home of *O. saundersii* and *O. humbertiana*, and the original range of *O. nigra* (apart from spreading by man) as from Egypt to India, the generic range extends from East Africa (*O. westwoodi*, Pleistocene, and *O. minuscula*) to Egypt, Mesopotamia, Arabia and India (*O. nigra*), with many species in the Indian region, including Burma, Malaya, Ceylon and South China (*O. asymmetrica*, *O. thoracica*, *O. greeniana*, *O. ceylonica*, *O. varians*, *O. borneensis*), *O. borneensis* extending through the East Indies to the Philippines, its northern congener (*O. japonica*) reaching to Southern Japan. To the south, the genus extends through New Guinea (*O. albertisi*) to Australia and Tasmania (*O. gurneyi*), with three very specialized endemic Western Australian species (*O. glauerti*, *O. tillyardi* and *O. approximans*). In the Indian Ocean, *O. scottiana* is confined to Mahé. The possibility of the entire absence of the genus from Africa, apart from distribution by man, has been suggested under *O. minuscula*.

Four species (*O. saundersii*, *O. humbertiana*, *O. nigra* and *O. greeniana*) appear to have the left cercus-basipodite distinct, with a process, and in addition a process on the left of the hypandrium (? left half of larval tenth sternite). The remaining species have an apparently composite structure, the distal part of the 'left cercus-basipodite' probably including the left half of the larval tenth sternite. If subgeneric division is required, the four subspecies listed above would form the type subgenus, and the name *Aposthonia* Krauss 1911 (genotype *O. borneensis*) could be used for the more closely inter-related of the remaining species (*O. japonica*, *O. varians*, *O. albertisi*, *O. scottiana*, *O. ceylonica*, *O. gurneyi*, and probably *O. minuscula*). The adoption of this subgenus would, however, lead to the undesirable splitting off of similar categories including (1) *O. tillyardi* and *O. approximans*;

(2) *O. glauerti*; (3) *O. thoracica*; (4) *O. westwoodi*; (5) *O. asymmetrica*. This course seems unnecessary, so that *Aposthonia* is not allowed even as a subgenus.

Key to the Species and Subspecies of Oligotoma (♂).

The following key, based on the characters of the mature males, serves to distinguish the species and subspecies recognized above:

1. First segment of left cercus with two inner lobes 2
   First segment of left cercus not as above 3
2. Lobes of left cercus placed one above the other, separated by a longitudinal groove ..... *minuscula* End.
   Lobes of first segment of left cercus placed one distad to other, the distal one long, beak-like ..... *asymmetrica* Men. et George.
3. Process of left hemitergite with a lateral lobe, not terminal 4
   Process of left hemitergite without such a lobe 5
4. Lateral lobe of process of left hemitergite oval, obtuse; first segment of left cercus produced inwards very strongly ..... *tillyardi* Davis.
   Lateral lobe of process of left hemitergite acute; first segment of left cercus produced inwards less strongly ..... *approximans* Davis.
5. Process of left hemitergite with a terminal hook 6
   Process of left hemitergite not as above 13
6. Termination of process of left hemitergite a bifid claw directed to the left ..... *humbertiana* (Sauss.).
   Termination of process of left hemitergite not as above 7
7. Termination of process of left hemitergite expanded into a weakly-bilobed lamina, with a small spine on the right ..... *greeniana* (End.).
   Process of left hemitergite not as above 8
8. Termination of process of left hemitergite a simple acute spine bent to the left 9
   Process of left hemitergite ending in an anchor-like hook ..... *glauerti* Till.
9. Right cercus-basipodite produced backwards; Pleistocene; length less than 4·5 mm. ..... *westwoodi* Hagen.
   Right cercus-basipodite small, subannular; Recent; length greater than 6 mm. .. 10
10. First segment of left cercus weakly clavate, inner margin smoothly dilated ..... *gurneyi subclavata* Davis.
    First segment of left cercus with inner margin produced to a process 11
11. Left cercus-basipodite fused to left side of hypandrium, terminally curved to the left as an acute spine ..... *gurneyi spinulosa* Davis.
    Left cercus-basipodite not as above 12
12. Outer process of right hemitergite apically bidentate ..... *gurneyi centralis* Davis.
    Outer process of right hemitergite simply tapered ..... *gurneyi gurneyi* Frogg.
13. Process of left hemitergite smoothly tapered, obtuse or subacute 14
    Process of left hemitergite obliquely truncate distally, slightly expanded ..... *thoracica*, n. sp.
14. Hypandrium with an acute sigmoid spine subterminally on the left; left cercus-basipodite a bilobed plate ..... *nigra* Hagen.
    Hypandrium and left cercus-basipodite not as above 15
15. Hypandrium with an acute subterminal spine arising on the left and curving under the hypandrium to the right, and upward terminally ..... *saundersii* Westw.
    Hypandrium without such a spine 16
16. First segment of left cercus strongly excavate on inner side in basal half; left cercus-basipodite weakly developed 17
    First segment of left cercus not as above; left cercus-basipodite stronger 18
17. First segment of left cercus produced inwards in a strong beak ..... *ceylonica indica*, n. subsp.
    First segment of left cercus not produced inwards strongly .. *ceylonica ceylonica* End.
18. Left cercus-basipodite terminally curved outwards in an acute hooklet 19
    Left cercus-basipodite obtusely tapered terminally 21
19. Outer process of right hemitergite with tooth on outer margin well back from apex ..... *scottiana* End.
    Outer process of right hemitergite not as above 20
20. Left cercus-basipodite broad, sigmoid ..... *varians* Navás.
    Left cercus-basipodite narrower, basally straighter ..... *borneensis* Hagen.

21. First segment of left cercus scarcely clavate; colour dark brown with thoracic nota yellowish; New Guinea ..... *albertisi* Navás.
First segment of left cercus markedly clavate; colour uniform brown; Japan and Formosa ..... *japonica* Okajima.

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THE SILURIAN RUGOSA OF THE YASS-BOWNING DISTRICT, N.S.W.

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(Plates xi–xiii; four Text-figures.)

[Read 28th August, 1940.]

In this paper eighteen species of Rugosa already described from the Yass-Bowning district are revised, and two genera and four species are described as new. Discussions are included of the families and genera involved. The age indicated by the Rugosa is Silurian, probably Upper Wenlock (Wenlock Limestone), and perhaps also Lower Ludlovian.

The Rugosa were collected chiefly from two localities, (1) Yass River, at Hatton's Corner, near Yass, and (2) Derrengullen Ck. and its tributary Limestone Ck., near Bowning. The lithological succession at both these localities has long been known; most of the corals have already been described by Etheridge, and some have more recently been revised by Jones. At Hatton's Corner, the Bowspring Limestone, up to 100 feet thick, is overlain by the Barrandella shales (about 70 feet thick), and these are followed by the Hume Limestone (20 feet). Further shales overlie the Hume Limestone, and are in turn overlain by the Phacops bed of very impure limestone of Rainbow Hill (Shearsby, 1912). For the Bowning district, the following succession at Bowning was given by Mitchell (Sussmilch, 1922, p. 36):

Conglomerates at top (tuffaceous matrix).
Shales and sandstones.
Conglomerates.
Shales and sandstones
Shales, sandstones, conglomerates } i.e. Upper Trilobite Bed.
Shales, i.e. Great Shale (Graptolites on west).
Limestone, impure (with trilobites), i.e. Middle Trilobite Bed.
Shales (with corals and crinoids), i.e. Lower Trilobite Bed (Graptolites on east).
Limestones (corals, brachiopods).
Grits at base.

Silurian graptolites from Silverdale near Bowning have recently been described (Sherrard and Keble, 1937, p. 306) as from the Lower Trilobite Bed[1] of Mitchell. Detailed field mapping of the sediments in the Silurian Yass-Bowning syncline is at present being undertaken by Dr. Ida Brown, Mr. A. J. Shearsby and members of the Geology Department of the University of Sydney. The Rugosa from a small outcrop of Silurian beds along the western bank of the Murrumbidgee between the Boambolo crossing and the Taemas Bridge are also recorded, one

[1] Sherrard and Keble have since considered (*in litteris*) that these graptolites may have come from the sandstone at the top of the Great Shale, where Mitchell collected *Orthis* and *Atrypa*.

new species being described. These beds are regarded as approximately of the same age as the Hatton's Corner beds.

The Rugose corals described herein are listed below, together with the Heliolitidae and the massive *Favosites*. Where any horizon at Hatton's Corner has been verified by me for these species, suitable letters are placed after them as follows: B.L. = Bowspring Limestone; B.S. = Barrandella Shale; H.L. = Hume Limestone; H.S. = Shales over Hume Limestone; P.B. = Phacops Bed of Rainbow Hill.

Ampleximorphs.

Pycnostylus congregationis (Etheridge), B.S.
dendroides (Etheridge), B.S.

Family Calceolidae.

Rhizophyllum interpunctatum de Koninck, B.S.
robustum Shearsby.
yassense Shearsby.

Cystimorphs.

Cystiphyllum sp. cf. *bohemicum* Pocta, B.L.
Holmophyllum multiseptatum, n. sp.

Family Disphyllidae.

Disphyllum praecox, n. sp., B.L.

Family Mycophyllidae.

Mycophyllum crateroides Etheridge, B.S.
liliiforme (Etheridge), B.S.

Family Pycnactidae.

Hercophyllum shearsbyi (Sussmilch), B.S.
Baeophyllum colligatum, n. gen. et sp., B.L.

Family Rhabdocyclidae.

Tryplasma delicatulum Etheridge.
derrengullenense Etheridge.
lonsdalei Etheridge, B.S.

Family Spongophyllidae.

Spongophyllum shearsbii Chapman, B.L., B.S.
spongophylloides (Foerste), B.L., H.L.
Yassia enormis (Etheridge), B.L.

Family Streptelasmidae.

Streptelasma australe (Foerste), P.B.

Family Entelophyllidae.

Entelophyllum latum, n. sp.
yassense (Etheridge), B.S., H.L.
yassense var. *patulum* (Foerste).

Rugosa Incertae Sedis.

Zenophila walli (Etheridge), B.S., H.L., H.S.

Heliolitidae.

Heliolites daintreei Nicholson and Etheridge, B.L.
Plasmopora heliolitoides Lindström. B.L.
gippslandica (Chapman).
Propora conferta Edwards and Haime, B.L.

Massive *Favosites*.

Favosites allani Jones, B.S.
gothlandicus forma *gothlandica* Lamarck. B.L., B.S.
libratus Jones.
regularis Jones, B.L., B.S.
richardsi Jones, B.S.
triporus Walkom, B.L., B.S.
yassensis Jones, B.S., H.L.

The Heliolitidae are described by Jones and Hill (1940), and the massive *Favosites* have been studied by Jones (1937). *Coenites intertextus* Etheridge, *Striatopora* and *Syringopora* also occur in the Yass district, while *Halysites* sp. is known from a quarry near Bango.

The Age of the Fauna.—Pycnostylus is known from the Guelph (Lower Ludlow) of Canada, and possibly from the Middle Devonian of Germany. *Rhizophyllum* ranges in Europe from the Wenlock to the Lower Devonian; *R. robustum* particularly is like *R. gotlandicum* from the Wenlock and Ludlow of Europe. *Cystiphyllum* sp. and *Holmophyllum multiseptatum* are comparable with European Wenlock and Ludlow forms. *Disphyllum* occurs elsewhere only in the Devonian. *Mycophyllum* has species comparable with ours in the Wenlock and Ludlow of Europe. *Hercophyllum* is very similar to *Lykophyllum westergardi* from the Stricklandinia marls (basal Wenlock) of Gotland. *Baeophyllum* may be like the Ludlow *Entelophyllum fasciculatum* from Gotland, or *Amplexus cingulatus* from the Niagaran of Quebec. *Tryplasma* has species comparable with ours in the Wenlock and Ludlow of Europe. *Spongophyllum spongophylloides* is comparable with the Wenlock (E_2) *S. inficetum* from Bohemia. *Yassia* is unknown elsewhere. *Streptelasma* is a very long-ranged genus, Upper Ordovician to Middle Devonian. *Entelophyllum* is Niagaran in America and Wenlock and Ludlow in Europe. *Zenophila* is not known elsewhere. The Rugosa thus prove a

Silurian age, nearly all forms having Wenlock and Ludlow affinities. This accords with evidence from the Silverdale graptolites (Sherrard and Keble, 1937, p. 307), which indicate for the bed containing them a horizon somewhere between the base of the Wenlock and the top of the Lower Ludlow. The narrowest comparisons that I can make are *Cystiphyllum* sp. to a Lower Ludlow form, *M. crateroides* to an Upper Wenlock specimen, *H. shearsbyi* to a basal Wenlock species, *B. colligatum* to a Ludlow specimen, and *S. spongophylloides* to an E_2 (approximately Wenlock limestone or Lower Ludlow) form. These suggest to me that the fauna represents the top of the Wenlock and perhaps also the base of the Ludlow.

The fauna contains Calceolidae, Cystimorphs, Pycnactidae, Rhabdocyclidae, Streptelasmidae and Entelophyllidae in common with the Wenlock Limestone of England, but *Arachniophyllum* and *Spongophylloides*, so characteristic in England, are lacking, and *Cystiphyllum*, common in England, is very rare at Yass, while the Ampleximorphs, *Disphyllum*, Mycophyllidae and Spongophyllidae, which form an important part of the Yass fauna, are not known in England. These differences appear to have a geographical rather than a time value, for Ampleximorphs, Mycophyllidae and Spongophyllidae occur in the Wenlock and Ludlow elsewhere in Europe. Disphyllidae are unknown elsewhere below the Devonian, of which they are characteristic.

Ampleximorphs.

Ampleximorphs are solitary or fasciculate Rugose corals which have thin walls, short lamellar septa and complete tabulae, and are without dissepiments.

Such corals could be the end-points of many different lineages, or trends in simplification. The absence of dissepiments is shared with the Rhabdocyclidae and the Mycophyllidae, but both these families have rhabdacanths in their septa, whereas in ampleximorphs the septa are lamellar and attenuate and short; only in rare instances may individual trabeculae be distinguished.

The Carboniferous *Amplexus* Sowerby, the Devonian *Cyathopaedium* Schlüter and *Cylindrophyllum* Yabe and Hayasaka, and the Silurian *Pycnostylus* Whiteaves and *Tabularia* Sochkina are regarded as among the ampleximorphs, and an examination of topotypes of all their genotypes would be needed for a proper understanding of their relations. Weissermel (1939, p. 14, 23) has recently made an important contribution by giving descriptions of the structure of the walls and septa in several forms, e.g. *Cyathopaedium paucitabulatum* (Schlüter). He has considered *Fletcheria* Edwards and Haime, from the Silurian of Gotland and Antirovitha, a genus which has many of the characters of ampleximorphs, to belong to the Tabulata and not to the Rugosa, as the structure of the walls and the nature of the septa is that of *Syringopora* or *Halysites*, spines set in a lamellar sclerenchyme. There are longitudinal furrows on the epitheca, as in the Rugosa, however, and Weissermel has stated that the genus may be close to the Rugose *Tryplasma* (a member of the Rhabdocyclidae). I am unable to accept the opinion of Lang, Smith and Thomas (1940, p. 112) that *Pycnostylus* is a synonym of *Fletcheria*, as the former appears to me to have lamellar septa. Weissermel also regards his "*Lyopora*" *amplexoides* from the high Upper Silurian of Antirovitha as a tabulate coral. It has similar general characters to those he described for *Fletcheria*, but has lateral increase in contrast to the calicinal increase of *Fletcheria*. There seems to be no generic identity between this species and the genotype *Lyopora favosa* Nicholson and Etheridge from the Craighead Limestone of Girvan, which possibly is related to *Calapoecia* Billings.

Genus PYCNOSTYLUS Whiteaves. Plate xi, fig. 1.

Pycnostylus Whiteaves, 1884, p. 2.—? *Cyathopaedium* Schlüter, 1889, p. 5, genotype *Calophyllum paucitabulatum* Schlüter, 1881, p. 190, Pl. ii, figs. 1–4; Stringocephalus beds (Givetian), Germany.—? *Cylindrophyllum* Yabe and Hayasaka, 1915, p. 90, genotype *Cylindrophyllum simplex* Yabe and Hayasaka, *id.*, 1920, Pl. vi, figs. 3*a*, *b*; Devonian, Yun-nan. (Non *Cylindrophyllum* Simpson, 1900, p. 217.)

Genotype, *Pycnostylus guelphensis* Whiteaves, 1884, p. 3, Pl. i, figs. 1–1*b*, Guelph (? Lower Ludlow), Hespeler, Guelph, Ontario. See also Lambe, 1901, p. 132, Plate x, figs. 4, 4*a*.

Diagnosis.—Phaceloid Rugose corals with axial increase, typically quadripartite, with thin walls, short lamellar septa and complete flat tabulae.

Remarks.—The diagnosis brings out a difference between the Australian corals placed herein, and those placed in *Tryplasma*. In *Tryplasma* the septa are acanthine, but in *Pycnostylus* they are lamellar. I have examined (by courtesy of Dr. A. E. Wilson) a topotype of *P. guelphensis*, and although it is dolomitized, I consider that it has short, lamellar septa as in ampleximorphs, and not short, rhabdacanthine septa as in *Tryplasma*. The Australian species have true amplexoid septa, i.e. very low prolongations from the peripheral lamellar portion continue along the upper surfaces of the tabulae towards the axis; such prolongations have not been observed in the topotype of *P. guelphensis*, but they may have been obscured by the dolomitization. Possibly the "extremely short spines" mentioned by Etheridge in the Australian specimens are to be explained as sections showing this discontinuity in the axial edges of the septa, rather than as sections of the rhabdacanths or holacanths of the Rhabdocyclidae. I have seen no evidence of such free trabeculae in either of the Australian species placed in the genus herein. Weissermel (1939, p. 14) has described the structure of the wall and septa in *Cyathopaedium*, and the similarity in these characters in the two genera indicates that they are synonymous.

The range of *Pycnostylus* is ? Lower Ludlow of Canada and Silurian of New South Wales, and, if *Cyathopaedium* be a synonym, extends into the Givetian of Germany.

PYCNOSTYLUS CONGREGATIONIS (Etheridge). Pl. xi, figs. 2*a*, *b*.

Tryplasma congregationis Etheridge, 1907, p. 84, Pl. xiii, fig. 1, Pl. xxi, fig. 10, Pl. xxiii, fig. 10; Silurian, Derrengullen Ck., Bowning district, New South Wales.

Lectotype (here chosen), F 8879, Australian Museum, figured Etheridge, 1907, Pl. xiii, fig. 1.

Diagnosis.—Phaceloid *Pycnostylus* with corallites 10 to 15 mm. in diameter, with numerous connecting processes arranged in tiers.

Description.—The corallum is very large, the corallites cylindrical or oval, 10 to 15 mm. in diameter, and unequally spaced. They show frequent growth constrictions and swellings. Connecting processes are numerous, at the same level in neighbouring corallites and more or less equally spaced at about 10 mm. apart. The epitheca shows fine growth annulation, but no or only very faintly marked longitudinal striation. Increase is probably peripheral, two offsets having been observed replacing one. There are 34 to 36 thin septa, lamellar and amplexoid, not acanthine. Straight axial prolongations extend over the upper surfaces of the tabulae almost to the axis, as very faintly marked ridges, but below the tabulae the septa are very short, less than 1 mm. The minor septa

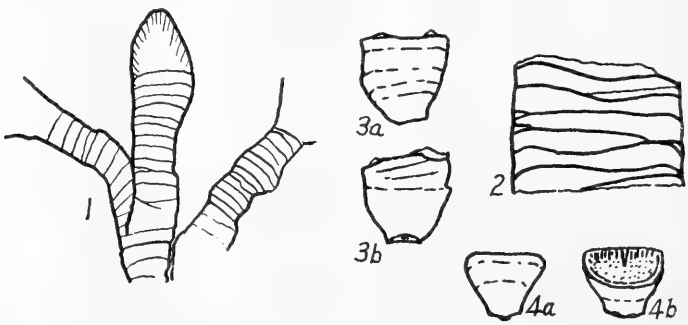
do not extend over the tabulae, and are less than 1 mm. in length. The tabulae are complete, with very slightly downturned edges.

Remarks.—The corallites of this species have a much greater diameter than in the genotype, but are approximately the same size as those of *P. dendroides*, which occurs with it, and which may indeed be but a forma of *congregationis*. Diagnostic structural differences between stems of *Mycophyllum liliiforme* and detached fragments of corallites of *P. congregationis* and *P. dendroides* have not been noted, and it might be that *P. congregationis* is really only an aggregation of stems of *M. liliiforme*, but they do not appear to be widely enough spaced to allow development of the calices of *M. liliiforme*, and the occurrence of offsets suggests they are not mere stems.

Localities.—In addition to the type locality, the species occurs at Hatton's Corner in the Barrandella shales.

PYCNOSTYLUS DENDROIDES (Etheridge). Text-figs. 1, 2.

Tryplasma dendroidea Etheridge, 1907, p. 87, Pl. xiv, fig. 1; Pl. xv, fig. 5; Pl. xviii, figs. 2–6; Pl. xix, fig. 6; Pl. xxii, figs. 11–15; Pl. xxiii, fig. 9; Pl. xxiv, fig. 6; Pl. xxvii, figs. 3, 4; Silurian, Derrengullen Ck., Bowning district, New South Wales.—Non *Tryplasma dendroidea* Etheridge, Hill, 1937, p. 151, text-fig. 9, grey limestone of Curradulla or Limestone Ck., New South Wales, which is *Tryplasma* sp. cf. *lonsdalei* Etheridge.



Text-fig. 1.—*Pycnostylus dendroides* (Etheridge). Outline drawing of exposed surface of lectotype, F 8895, Australian Museum Collection; Silurian, Barber's Ck., off Derrengullen Ck., near Bowning. × ¾.

Text-fig. 2.—*Pycnostylus dendroides* (Etheridge). Drawing of vertical section figured by Etheridge, 1907, Pl. xxiv, fig. 6. × 1½.

Text-fig. 3.—*Rhizophyllum interpunctatum* de Koninck. Outline drawings from Etheridge's figures (1881, fig. 7) of a syntype, now missing, of his *Rhizophyllum australe*. Silurian, near Yass. × ¾. 3*a*, flat face; 3*b*, semicircular face.

Text-fig. 4.—*Rhizophyllum interpunctatum* de Koninck. Outline drawings from Etheridge's figures (1881, fig. 8) of a syntype, R 33579, British Museum (Natural History) Collection, of his *Rhizophyllum australe*. Silurian, near Yass. × ¾.

Lectotype (here chosen), F 8895, Australian Museum, figured Etheridge, 1907, Pl. xv, fig. 5. Silurian, Barber's Ck. (a branch of Derrengullen Ck.).

Diagnosis.—Dendroid *Pycnostylus* with quadripartite axial increase, the offsets diverging, the corallites being 12 mm. in average diameter.

Description.—The corallum is dendroid, the corallites being 12 mm. in average diameter, expanding to 15 or 20 mm. just before increase, which is usually quadripartite and axial. The offsets diverge. The epitheca shows fine growth

annulation. Connecting processes occur rarely. The septa are about 55, the minor being indistinguishable from the major in section, where all are about 1 mm. long. They are lamellar, not acanthine, and are amplexoid, as in *P. congregationis*. The tabulae are complete, with slightly downturned edges, rather distant.

Remarks.—As Etheridge has already remarked, the species closely resembles *P. congregationis* in size of corallite and nature of septa and tabulae, but differs in the growth form, being dendroid instead of phaceloid, and in the number of septa, Etheridge having observed nearly twice as many septa in *P. dendroides* as in *P. congregationis*. It seems to me probable that the two are simply growth forms of one species, and that the smaller number of septa counted by Etheridge in *P. congregationis* was due to his having used only a small corallite of this species, as I have counted 54 septa in a corallite of 12 mm. diameter in *P. congregationis*. But this must await confirmation by field studies.

The possibility that the corallites of *P. dendroides* are merely the stems of *Mycophyllum liliiforme*, which is suggested by general structure, is discounted by the arising of four new corallites from an old one, by axial increase. It is thought unlikely, but not perhaps impossible, that mere stems would show such increase.

The specimen in the Sedgwick Museum, from the W. B. Clarke Collection, which I called *T. dendroidea* (Hill, 1937, p. 151, text-fig. 9) now appears to me to be a true *Tryplasma*, as it has the rhabdacanthine septa of that genus, whereas the type of *P. dendroides*, which I have since examined, has amplexoid, lamellar septa. The Sedgwick Museum specimen has stouter corallites than is usual in *T. lonsdalei*, but it is here transferred doubtfully to that species.

Localities.—In addition to the type occurrence, the species is found in the Silurian Barrandella shales of Hatton's Corner, Yass R., N.S.W.

Family Calceolidae.

Typical genus, *Calceola* Lamarck, 1799, p. 89.

Calceoloid Rugosa with a semi-circular operculum.

Range.—Wenlock and Ludlow of Europe, Asia, North America and Australia, Lower Devonian of France, and Middle Devonian of Europe, Asia and Australia.

Remarks.—Lindström (1883, p. 9), the founder of the family, placed in it the Middle Devonian *Calceola*, the Chinese Wenlock and Russian Gedinnian and Eifelian *Platyphyllum* Lindström (1883, p. 40), the widespread Wenlock to Lower Devonian *Rhizophyllum*, and the English and Scandinavian Wenlock and Ludlow *Goniophyllum* Edwards and Haime (1850, p. lxix), the first three forming one sub-group, and the last a second sub-group. In the diagnosis given above, *Goniophyllum* is excluded from the family, as it differs not only in being prismatic instead of semi-circular in section, and in having four opercula instead of one, but also in septal structure; the septa of *Goniophyllum*, being dilated lamellar, suggest relationship to the Pycnactidae rather than to *Rhizophyllum*, which has semi-acanthine septa. It is possible that *Calceola* was derived from *Rhizophyllum* through *Platyphyllum* by the gradual thickening of the skeletal elements, though the structure of the septa in *Platyphyllum* has never been clearly figured. *Calceola glossophylloides* Sochkina (1936, p. 69), from the Eifelian of the Northern Urals, may be *Platyphyllum*, as the figures show dilated, arched plates.

Lindström united his family Calceolidae with another, the Araeopomatidae, also with opercula, into the Anthozoa operculata; but all of these corals have the septal arrangement of the Rugosa, so that they are Anthozoa rugosa; an operculum

may have been evolved in many lineages, and Lindström's Operculata is most probably polyphyletic. Lindström remarked on the possible homology of the opercula with the epithecal scales found in *Tryplasma*, and Smyth (1933) has recently described epithecal scales in Carboniferous Tabulata. The arrangement of the internal plates in *Rhizophyllum* and *Platyphyllum* and the semi-acanthine nature of the septa in *Rhizophyllum* suggest comparison with *Cystiphyllum*.

Genus Rhizophyllum Lindström.

Rhizophyllum Lindström, 1866*a*, p. 279; 1866*b*, p. 411; 1883, p. 22.

Genotype (by designation, Lindström, 1866, p. 411), *Calceola gotlandica* F. Roemer, Silurian, Gotland.

Diagnosis.—Calceoloid corals with semi-circular operculum; with undilated, arched horizontal skeletal elements, none of which extend completely across the lumen, and with vertical skeletal elements reduced to a series of short septa, partly lamellar and partly acanthine, on the flattened side of the corallum.

Range.—Gotlandian of Gotland and England, Asia, North America and Australia, and Lower Devonian of France.

Remarks.—Two Ludlovian species, *R. elongatum* Lindström from Gotland, and *R. attenuatum* Lyon from North America, are compound, the former by calicinal increase, the latter by stolonal increase. *R. tenesseense* F. Roemer is without rootlets, but all other described species have them.

Rhizophyllum interpunctatum de Koninck. Pl. xi, figs. 4–10; text-figs. 3, 4.

Rhyzophyllum interpunctatum de Koninck, 1876, p. 61, Pl. i, fig. 14; Silurian, Rock Flat Ck., Manero, N.S.W.—*Rhyzophyllum? interpunctatum, loc. cit.* Explanation to plates.—*Rhizophyllum australe* Etheridge, 1881, p. 248, figs. 7, 8; Silurian, Yass, N.S.W. A type for this cannot at present be chosen. See under remarks.—*R. australe* Etheridge, 1891, p. 202 *pars*, i.e. Pl. xxx, figs. 4–6; Silurian, Hatton's Corner, Yass R., N.S.W.—*R. interpunctatum*, Etheridge, 1891, p. 203, Pl. xxx, figs. 7–15; Silurian, Hatton's Corner, Yass R., N.S.W., and Silverdale, near Bowning.—*R. australe*, Shearsby, 1906, p. 549, Pl. xxvi, figs. 8, 23, 24; Silurian, Hatton's Corner, Yass R.—*R. interpunctatum*, Shearsby, *id.*, figs. 9–18, 20–22; Silurian, Hatton's Corner, Yass R.

Type Material.—De Koninck's specimens were lost in the Garden Palace Fire at Sydney, 1882. The type locality has not been revisited, and no topotypes are available, so that it is not possible to choose a neotype. From de Koninck's figure it seems reasonably certain that the specimens from Yass described below are conspecific with the Rock Flat specimen, and the following diagnosis and description are based on them.

Diagnosis.—*Rhizophyllum* attaining a diameter of 10–15 mm. in a height of from 10 to 20 mm., and thereafter a fairly constant diameter, with or without rejuvenescence.

Description.—The calceoloid corallum is usually curved, so that the flat surface is longer than the semi-circular surface. When the curvature is great, the calical margin (which during growth appears to have remained approximately parallel to the sea-floor) is oblique to the flat surface; when curvature is small the calical margin is approximately at right angles to the flat surface. The average maximum diameter is 15 mm.; when this is attained the corallum ceases to grow in width as it grows in height, or rejuvenescence may occur. The proximal expanding portion of a corallum is turbinate or trochoid. The epitheca shows growth annulation, and sometimes a longitudinal ridge in the middle of

the flat face, less frequently in the middle of the semi-circular face also. The junction of the flat and semi-circular faces may be at a sharp or rounded angle. The calice has its deepest part near the middle of the semi-circular face, the curvature of its floor increasing very rapidly into this pit. Septa are usually visible along the flat edge, the counter septum being large, and extending half-way to the eccentric axis (the calicular pit); they are in two series, the minor being 1 or 2 mm. long, while the major septa increase in length from the angles towards the counter septum. In moulds of the calice the furrows left by the septa and the intervening ridges bear minute granules, and these continue down into the calicular pit after the septal furrows have died away. Rootlets arise from the lateral angles, and some few from the proximal parts of the flat face. The operculum is semi-circular, with a notched median ridge on its lower surface at the flat edge, and bears ridges and furrows spreading out to the semi-circular edge from the flat edge, being most marked at the flat edge. It consists of dense sclerenchyme.

In thin section, the corallum is seen to consist of small domed plates, those between major and minor septa at the flat surface being smaller and more horizontally based than the others, which are inclined parallel to the floor of the calice. Dilatation of the domed plates may occur periodically on the floors representing previous positions of the calice. Septa are seen at the flat surface as short, sometimes thickened plates, sometimes represented by discrete trabeculae.

Remarks.—Etheridge (1881) founded the species *R. australe* on three syntypes collected by Liversidge from Yass. One syntype, that figured fig. 7, is missing; that figured fig. 8 is R33579 in the British Museum (Natural History), London; the third, unfigured, is 90285 in the British Museum. Since lectotypes must be chosen from syntypes, if available, one of these three must be used for the interpretation of *R. australe*. R33579 is not desirable, since Etheridge removed it from the species (1891) into *interpunctatum* de Koninck; 90285 is not at present available, so that one cannot be sure of its characters; the third is missing. Consequently no lectotype can be chosen herein. Etheridge in 1891 considered that two species could be recognized amongst the smaller *Rhizophyllum* of Yass, one, *R. interpunctatum*, in which the corallum was broader, and less erect, and had more noticeable septa than the other, to which he restricted his name *R. australe*, although his description and figures in 1881 both referred to the broader coralla. I have examined many individuals from Yass, however, and have found all variations in size between the two limits mentioned in my diagnosis; variation in the periodic dilatation of old calical floors is great; variation in the strength of the septa also occurs, and I have not found that strong septa are always more noticeable in the broader coralla, nor that the broader coralla are always the more curved. All the specimens I have seen I regard as one species, *R. interpunctatum*. Nevertheless I have not seen any specimen with quite such elongate proportions as $7\frac{1}{2} \times 22\frac{1}{2}$ mm., as figured by Etheridge, 1891, figs. 1–3, and it might be that this specimen is a species distinct from all the others. On the other hand, it may only represent the limit of variation of the Yass species, which appears most reasonably referable to *R. interpunctatum* de Koninck.

The species is smaller than *R. gotlandicum* (Roemer), from the Gotlandian of Europe, but is otherwise very similar to it.

Localities.—In addition to the localities mentioned in the synonymy, the species occurs in a bed of impure limestone in Derrengullen Ck., a few hundred yards above the Yass-Wargeila road crossing.

RHIZOPHYLLUM ROBUSTUM Shearsby. Plate xi, figs. 11*a*, *b*.

Rhizophyllum robustum Shearsby, 1906, p. 548, Pl. xxvi, figs. 1–6, 19; impure limestone on the Wargeila road about ½ mile west of Yass Junction railway station; impure coral limestone, Derrengullen Ck., a few hundred yards above the Yass-Wargeila road crossing. Silurian.

Lectotype (here chosen), F 37056, Australian Museum, figd. Shearsby, *loc. cit.*, figs. 1–6; impure limestone on the Wargeila road about ½ mile west of Yass Junction railway station. Silurian.

Diagnosis.—Large turbinate, erect *Rhizophyllum* with calice about 29 × 16 mm., at a height of about 29 mm.

Description.—The corallum is turbinate and erect, and may have a distal portion which grows in height, without increase in diameter; the calice is 38 × 20 mm. in a large specimen from Limestone Ck. The calical margin is at right angles to the ventral face (as is usual in calceolids when the corallum is erect). The characters of the calice, the epitheca, and the internal structure including the position of the calicular pit, are as described above for *R. interpunctatum*. Hollow cylindrical rootlets may occur on the flat face and at the lateral angles.

Remarks.—This species closely resembles *R. gotlandicum* (Roemer) from the Wenlock and Ludlow of Gotland, and may indeed be a synonym. It differs from *R. interpunctatum*, with which it occurs, only in size and in being erect; but specimens forming a gradational series in size between the two have not been found.

Localities.—In addition to the localities mentioned in the reference, the species occurs at Limestone Ck., a tributary of Derrengullen Ck., in the Silurian.

RHIZOPHYLLUM YASSENSE Shearsby. Plate xi, figs. 12*a*, *b*.

Rhizophyllum yassense Shearsby, 1905, p. 869, Pl. xxvi (xxvii); Silurian. Shales in Derrengullen Ck. at the junction with Limestone Creek, near Bowning, N.S.W.—*R. yassense*, Shearsby, 1906, p. 549, Pl. xxvi, fig. 7.

Monotype, Australian Museum, F 37055, figured Shearsby, *loc. cit.*

Diagnosis.—Widely expanded *Rhizophyllum* of sub-oval section, erect at first, and curved distally, with calicular pit sub-central.

Remarks.—Only the holotype is known. It is 20 mm. tall, and the calice is 42 mm. × 20 mm. The flat surface is pinched in near the calice, so that the calical margin is a crescentic oval. The position of the calicular pit, sub-central instead of just inside the middle of the semi-circular face, is unusual. The other species from Yass all have this calicular pit in the normal position. The septa are but faintly distinguishable, but the lumen is filled with the small domed plates typical of the genus. A few bases of rootlets are visible on the flat face near the lateral angles. It may be that this specimen is a malformed individual of *R. robustum*, as no other specimens have been found with the crescentic calice and excentric pit.

CYSTIMORPHS.

Cystimorphs, Hill, 1939*b*, p. 248.

Genus CYSTIPHYLLUM Lonsdale.

Cystiphyllum Lonsdale, 1839, p. 691, see Lang and Smith, 1927, p. 455.

Genotype, *Cystiphyllum siluriense* Lonsdale, 1839, p. 691, Pl. xvi, figs. 1, 1*a*, *non* fig. 2; Wenlock Limestone, Wenlock and Dudley.

Diagnosis.—Rugose corals in which the vertical skeletal elements are represented entirely by holacanths and the corallum is constructed almost entirely of arched horizontal skeletal elements, none of which extend completely across the lumen.

Range.—Silurian of Europe, N. America and Australia.

CYSTIPHYLLUM sp. cf. BOHEMICUM Počta. Plate xi, figs. 13*a*, *b*.

Material.—F 3554–7 University of Queensland Collection, Bowspring Limestone, Hatton's Corner, Yass R., N.S.W. Silurian.

Diagnosis of Yass specimens.—Large trocho-cylindrical *Cystiphyllum* with a wide tabularium of large and frequently complete tabulae.

Description.—The largest specimen, which is unevenly weathered, is 9 cm. long and 3·5 cm. in diameter, but as most of the dissepimentarium is weathered away, the actual diameter must have been considerably greater. All of the specimens have been worn before fossilization, and in some only the tabularium remains. No septal spines are visible in the only transverse section obtained. The dissepiments are moderately large and are steeply inclined, and the unweathered dissepimentarium was at least 12 mm. wide. The tabularium is 20 mm. or more in diameter, and the tabulae are large, arranged in concave floors, some being complete, but many being represented by several tabellae, which are rather globose.

Remarks.—These large incomplete specimens resemble *Cystiphyllum siluriense* from the Wenlock Limestone of Wenlock (Lang and Smith, 1927, p. 476) and *C. bohemicum* Počta (1902, p. 164) from E_2 (Lower Ludlow) of Tachlowitz very closely. They appear closer to *C. bohemicum* because of the great coarseness of their tabular tissue. More specimens are required for an accurate specific evaluation.

Genus HOLMOPHYLLUM Wedekind.

Holmophyllum Wedekind, 1927, p. 30.—*Hedstromophyllum* Wedekind, 1927, p. 64, genotype *Hedstromophyllum articulatum* Wedekind, 1927, p. 65, Pl. 21, figs. 1, 2, Pl. 26, figs. 6–12; Gotland, Horizon III (Lower Ludlow).

Genotype (by monotypy), *Holmophyllum holmi* Wedekind, 1927, p. 31, Pl. 4, figs. 6–8, Pl. 29, fig. 16; Lau beds (Lower Ludlow), Gotland.

Diagnosis.—Cystimorphs in which the discontinuous acanthine trabeculae each pierce several dissepiments or tabulae.

Remarks.—The morphology of *Hedstromophyllum* seems to be identical with that of *Holmophyllum*, although Wedekind considered the former a descendant of *Cystiphyllum*, and the latter a descendant of *Tryplasma*. *Holmophyllum*, however, does not show the double septal ridges on the epitheca so characteristic of *Tryplasma* and, like *Cystiphyllum*, it has a dissepimentarium, which is lacking in *Tryplasma*. In addition to the Ludlow forms mentioned by Wedekind and by Alexander (1936, p. 107), and the Salopian species described by Lewis (1934, p. 96), I have seen a species from the Woolhope Limestone of Woolhope. The range of the genus would thus appear to be Middle and Upper Silurian.

HOLMOPHYLLUM MULTISEPTATUM, n. sp. Plate xi, figs. 14*a*, *b*.

Holotype, F 1023, University of Queensland Collection, said to be from Cliftonwood, near Yass. This is the only specimen known.

Diagnosis.—Trochoid *Holmophyllum* with very numerous septa.

Description.—The corallum is trochoid, expanding to a diameter of 35 mm. in a height of 55 mm., somewhat flattened, and nearly erect. Growth expansions and contractions are frequent. There are about 180 septa represented by single radial series of discrete trabeculae. The septa appear to be divisible into major and minor septa, but so close are the radial series of trabeculae that it is difficult to be certain of this. The trabeculae of a series are frequently connected by dissepiment-like plates. The arrangement of fibres in the trabeculae cannot be ascertained, but some of the trabeculae are elongated across the length of the septum. The longer septa reach almost to the axis, and the shorter extend half-way or less than half-way. The dissepiments are close, rather small elongate plates, lying approximately horizontally near the periphery, but descending steeply towards the tabularium. The tabularium is about 8 mm. wide at a diameter of 35 mm. The tabular floors are concave and the tabellae are small, closely packed and rather elongate. In vertical section the trabeculae can be seen piercing the dissepimental tissue, running at right angles to the course of the dissepiments.

Remarks.—This species is much larger than any of the described European species of the genus, and the septa appear to be more numerous. The age indicated would be within the range of the genus, Wenlock or Ludlovian.

Family Disphyllidae (Hill, 1939*a*, p. 224).

Genus Disphyllum de Fromentel.

Disphyllum de Fromentel, 1861, p. 302; Lang and Smith, 1935, p. 544; Hill, 1939*a*, p. 224.

Genolectotype (chosen Lang and Smith, 1934, p. 80), *Cyathophyllum caespitosum* Goldfuss, 1826, Pl. xix, fig. 2*b*. Middle Devonian, Eifel; renamed *Cyathophyllum goldfussi* Geinitz, 1846, p. 569. See Lang and Smith, 1935, p. 568.

Diagnosis.—Phaceloid Rugose corals in which increase may be lateral or peripheral; the septa rarely reach the axis, but are usually long, and typically thin; the tabulae are sometimes complete, though generally incomplete and differentiated into a transverse axial, and an inclined periaxial series; with dissepiments typically small, strongly arched, sometimes of one, but frequently of two, kinds: an inner, single series of globose, distally directed dissepiments, and an outer series of flat or arched dissepiments.

Remarks.—In Europe and North America the genus is characteristic of the Middle and Upper Devonian. In Australia it occurs in the Silurian (Wenlock or Ludlow), Lower and Middle Devonian.

Disphyllum praecox, n. sp. Plate xi, figs. 15–17.

Holotype, Australian Museum F 9709, with two thin sections A.M. 745. Shale in Limestone Creek, 50 yards below the Bowning–Wargeila road crossing. Silurian.

Diagnosis.—*Disphyllum* with major septa somewhat withdrawn from the axis, and minor septa half as long; with complete, slightly domed tabulae, and rhomboid or very globose dissepiments.

Description.—The corallum is sub-phaceloid or almost spreading, increase being peripheral, usually four new corallites appearing at once, killing the parent. Connecting processes occur, and when the corallites are in contact they may be partly cerioid. The average adult diameter is 15 mm., but it may be larger just before increase. There are 20 to 22 septa of each order, the major septa extending from one-half to two-thirds of the distance to the axis, so that an axial space is left. The minor septa are only half as long as the major septa. Both orders are attenuate, and rather wavy, sometimes with extremely short carinae. The tabulae

are complete and very slightly domed, or sometimes saucered, rather evenly spaced, about 10 in 5 mm. Usually only one series of dissepiments is present, consisting of plates which are flattened at the periphery, extend inwards for a greater distance than their height, and then curve down with a swollen curve to meet the plate below, so that in vertical section they look like a series of rhombs. When more than one series of dissepiments are developed, they are very globose, almost horseshoe-shaped.

Remarks.—This, the only known Silurian species, is closest to *D. gemmiforme* Etheridge from the Devonian of the Yass district, but the latter differs in having the major septa as short as the minor septa and a more spreading growth. Two species from the Lower Middle Devonian Nevada limestone, *Spongophyllum nevadense* Stumm (1937, Pl. 55, fig. 5) and *Spongophyllum expansum* Stumm (*id.*, fig. 6) somewhat resemble these Australian Disphyllids, but the minor septa are discontinuous. They may also be *Disphyllum*.

Localities.—This species occurs in the Silurian of the Yass district at the following places in addition to the type locality: Por. 35, Par. Derrengullen. On the south bank of the Yass R. in Por 84, Parish of Waroo (Station 61), F 8633, A.M. 624, Australian Museum Collection. Bowspring Limestone, Yass, S 9, F 179, O. A. Jones Collection, University of Queensland. Por. 161, Parish of Yass (Station 108, Yass R.), F 9719, A.M. 744, Australian Museum Collection. Limestone Ck., Bowning district, F 9879, Australian Museum Collection.

There are also specimens which may belong to this species in the University of Queensland Collection from Parkes road, Wellington, N.S.W., collected by O. A. Jones and A. K. Denmead.

Family Mycophyllidae, Hill, 1940, p. 156, *q.v.*

Genus Mycophyllum Etheridge.

? *Aspasmophyllum* F. Romer, 1880, p. 184. Monotype, *Aspasmophyllum crinophilum* Romer, *id.* [Middle] Devonian, [possibly crinoid beds at base of Givetian, Gerolstein], the Eifel.—*Mucophyllum* Etheridge, 1894, p. 11.—Lang, Smith and Thomas, 1940, p. 87, have corrected the spelling to *Mycophyllum*.

Genotype (by monotypy), *Mucophyllum crateroides* Etheridge, *id.*, Pls. iii, iv. Silurian, [Hatton's Corner, Yass R.], N.S.W.

Diagnosis.—Simple or sub-compound Rugose corals with expanded calical rims; with the approximately equal major and minor septa dilated and in contact so that dissepiments are entirely suppressed, and with complete and distant tabulae.

Remarks.—The genus is here understood to include those Mycophyllidae with expanded calical rims. I place in it, besides the genotype, *Tryplasma liliiforme* Etheridge, described below, which has a narrower stem-like portion below the calice, and is sub-compound, *Pseudomphyma atava* var. *expansa* Wedekind (1927, p. 38, Pl. vii, figs. 4, 5) and *Pseudomphyma turbinata* Wedekind (*id.*, Pl. viii, fig. 7, Pl. vi, figs. 1, 2), solitary forms with broad stems from the Ludlovian of Gotland, *Pseudomphyma expansa* Wedekind, Sochkina (1937, p. 56) from the Middle Ludlow of the Urals, another solitary form, and *Amplexus* (*Coelophyllum*) *eurycalyx* Weissermel (1894, p. 634) from the diluvial of Germany, a sub-compound species. Another form with an expanded calical rim is *Aspasmophyllum crinophilum* from the Middle Devonian of Germany; but it is insufficiently figured, and one cannot be sure that *Mycophyllum* is synonymous with it, although this seems likely.

Septal Structure.—In his description of *Mycophyllum*, Etheridge mistakenly considered the lines of junction of the dilated septa to be attenuate septa, and thus failed to recognize the similarity between *M. liliiforme* and *M. crateroides*. As in

the other Mycophyllidae, the dilated septa consist of rhabdacanths, in which the 'rods' diverge from the axis in a very broad curve, directed on the average at about 30° from the axis. The rods are fairly widely spaced, and all are set in a lamellar sclerenchyme which is parallel to the distal surfaces of the septa, and is not continuous from one septum to the next. The rhabdacanths are about 1 mm. apart. In the expanded calical rim the rhabdacanths are directed at right angles to the upper and lower surfaces of the rim. The septal structure has been well illustrated by Lang (1926, p. 431, Pl. xxx, figs. 7, 8).

MYCOPHYLLUM CRATEROIDES Etheridge. Plate xii, figs. 1, 2.

Mucophyllum crateroides, Etheridge, 1894, p. 18, Pls. iii, iv; Hatton's Corner, Yass R.; Old Limekiln Ridge, Humewood, near Yass; Quedong, Delegate R., Co. Wellesley, N.S.W. Silurian.—Lang, 1926, p. 433, Pl. xxx, figs. 7, 8.

Lectotype (here chosen), F 3048, Australian Museum Collection, figured Etheridge, *loc. cit.*, Pl. iv, fig. 3, Humewood.

Diagnosis.—Solitary, patellate *Mycophyllum* with broad, thick, slightly everted, expanded calical rim, and short, conical stem.

Description.—The corallum is solitary, attached and large, patellate, with expanded calical rim which is broad, thick and slightly everted. It may be 115 mm. in diameter and 80 mm. tall, but the average size is rather less. In a corallum 80 mm. in diameter, the calical rim was 30 mm. wide, and 11 mm. thick in its thickest part, which was midway between the periphery and the axial calicular pit corresponding to the tabularium. The edge of the calical rim is scalloped, the undulations occurring at the junctions of the septa. Rootlets may occur irregularly on the under surface. The axial calicular pit may be about 15 mm. wide. The cardinal fossula is a deeper indentation at the edge of the calicular pit.

There are 75 to 80 septa, the major not being distinguishable from the minor, dilated, and in contact throughout their length. The junction line of two septa is irregular, showing in section as a thin, very wavy line. In the proximal cone they are extremely short, but they form the entire expanded calicular rim. The septa consist of rhabdacanths set in lamellar sclerenchyme, the dimensions and arrangement being as remarked under the genus. The tabularium is the short, broadly conical "stem" below the expanded calice, and the tabulae are complete, flat and rather distant, and may be much dilated. They are sometimes dilated, and in a thin transverse section (Australian Museum 796) taken through the thickening on a tabula, shadows indicate that the thickening is septal in origin, the septa being excessively dilated and in contact. It appears further that the major septa were long and extended approximately to the axis. This length of the septa only in the thickening above the tabulae shows that the septa are amplexoid, i.e., perfectly developed only on the upper surfaces of the tabulae, and then between tabulae are withdrawn towards the periphery. The rootlets are thick-walled and hollow or crossed by transverse partitions.

Remarks.—Of the foreign representatives of the genus, specimen A 6269 in the Sedgwick Museum, Cambridge, from the Slite-gruppen, Gotland, is the closest to *M. crateroides*. It has a wider fossula and a thicker rim, but these are the only observable differences. This Upper Wenlock specimen may be *Pseudomphyma patellata* Wedekind (1927, p. 38), which is unfigured, from horizon IVb of Hedström (Ludlow).

Localities.—I have seen specimens from the Silurian of Hatton's Corner, Yass R.; Humewood, near Yass; and from Spring Ck., near Mt. Canoblas, N.S.W.

MYCOPHYLLUM LILIIFORME (Etheridge). Plate xi, figs. 18, 19; Plate xii, figs. 3–6.

Tryplasma liliiformis Etheridge, 1907, p. 95, Pl. xiv, figs. 2, 3; Pl. xv, figs. 2, 3 (*non* fig. 4); Pl. xvii, figs. 7, 8; Pl. xxiv, fig. 1; Pl. xxv, fig. 8; Pl. xxvii, figs. 1, 2; from Barber's Ck. and Derrengullen Ck.; Hatton's Corner, Yass R.; East bank, Yass R., Por. 103, Par. Waroo (NE corner); Por. 106, Par. Barton, Co. Ashburnham, near Mt. Canoblas. Silurian.

Lectotype (here chosen), F 8892, Australian Museum, Silurian, Barber's Ck., off Derrengullen Ck., Bowning district. Figured Etheridge, *loc. cit.*, Pl. xv, fig. 3.

Diagnosis.—Subcompound *Mycophyllum* with turbinate or trochoid stem, and thin, spreading calical rim; with occasional peripheral increase.

Description.—The corallum may be sub-compound, some offsets arising from the calicular rim. The corallite is liliaciform, with a turbinate or trochoid stem (the tabularium) below, and an expanding, bell-shaped calical rim. The rim is never everted, though the curvature from the stem usually increases upwards and outwards. The rim remains thin, from 1 to 2 mm.; it may be 25 mm. wide, in a calice 60 mm. in diameter. Sections are sometimes observed indicating that a broadly curved operculum may be present over the top of the calice, of the same thickness as the calicular rim. Rootlets are sometimes on the stem.

There are about 80 dilated septa in a large calice, the major being just distinguishable from the minor. Each septum may be from 1 to 1·5 mm. wide at the edge of the calice. They are very short in the stem between the tabulae and in the calice they are so dilated that the bell walls consist entirely of them. They are rhabdacanthine, the ends of the rhabdacanths projecting a little as spines at the inner edges, particularly near the calicular pit. The tabularium may be 20 mm. wide at the base of the calice, and the stem-like portion extends downwards, sometimes with rapidly decreasing diameter, sometimes slowly decreasing, the longest incomplete stem observed being 20 mm. at the top and 12 mm. at the broken base. The tabulae are complete, horizontal and rather distant, or incomplete and rather irregular.

Localities.—Those given in the reference above.

Remarks.—Etheridge considered this form a *Tryplasma* because of the spines usually present at the inner edges of the septa. The species may indeed be distantly related to *Tryplasma*, but its morphology is that of the Mycophyllidae, and it is very close to *Mycophyllum crateroides*. Etheridge missed the resemblance because he considered the wavy lines of junction between the dilated septa of *crateroides* to be true, attenuate septa. *M. liliiforme* is, as Etheridge pointed out, very similar to *Amplexus eurycalyx* Weissermel from the diluvial of Germany. It is also somewhat similar to species from the Ludlovian of Gotland placed in *Pseudomphyma* Wedekind (1927, p. 38). It is possible, see above, p. 393, that "*Tryplasma dendroides* Etheridge" and "*Tryplasma congregationis* Etheridge" may be the stems of *M. liliiforme*.

Family PYCNACTIDAE.

Typical genus, *Pycnactis* Ryder, 1926.

Solitary Rugose corals in which the septa are dilated in the tabularium, and thin in the dissepimentarium, when this is developed; with incomplete tabulae, usually inclined downwards to an excentric axis; dissepiments when present are typically small and neither flattened nor globose.

Range.—Silurian of Europe and New South Wales.

Remarks.—The family is important in the Silurian of Britain and the northern European countries, and is represented also in New South Wales. The British

members are all to be referred to the genera *Pycnactis* Ryder (1926, genotype *Hippurites mitratus* Schlotheim), *Mesactis* Ryder (1926, genotype *Mesactis glevensis* Ryder), *Phaulactis* Ryder (1926, genotype *Phaulactis cyathophylloides* Ryder from the Slite Gruppen of Westergarn, Gotland) and *Lamprophyllum* Wedekind (1927, pp. 76, 78, genotype *L. de-geeri* Wedekind, 1927, p. 78, Pl. xxviii, figs. 1–4, from the Silurian marls of Petesvik, Gotland). Probably *Mesactis* is superfluous. It was intended for individuals whose neanic stages were intermediate between those of *Pycnactis mitratus* and *Phaulactis* in the development of the horizontal skeletal elements, but the holotype of *P. mitratus* has some dissepiments already developed (*fide* Smith) and forms with only a few dissepiments can thus be placed in *Pycnactis*; other individuals with more dissepiments may be regarded as *Phaulactis*.

Scandinavian forms have recently been studied by Wedekind (1927) and Vollbrecht (1928), and from their figures it seems to me that the following belong to the Pycnactidae. Their genotypes are given in the Index, of Lang, Smith and Thomas. (1) *Lycophyllum* Wedekind (1927, p. 68); (2) *Lycocystiphyllum* Wedekind (1927, p. 73); (3) *Aulacophyllum* of Wedekind (1927, p. 74), *non* Edwards and Haime; (4) *Semaeophyllum* Vollbrecht MS in Wedekind (1927, p. 12); (5) *Desmophyllum* Wedekind (1927, p. 76), *non* Ehrenberg; (6) *Neocystiphyllum* Wedekind (1927, p. 77); (7) *Lamprophyllum* Wedekind. From the figures it seems that *Aulacophyllum* of Wedekind is a synonym of *Pycnactis*. *Plasmophyllum* of Lang and Smith (1927, p. 458), *non* Dybowski (see Lang, Smith and Thomas, 1940, p. 101) is a synonym of *Lamprophyllum*. All of the others might well be synonyms of *Phaulactis*, but it is difficult to take full account of the generic value of the differences described by Wedekind without examination of his actual material. The criteria on which he relies are the manner and position in which the thickened parts of the septa thin during ontogeny, and the nature of the tabulae (complete or incomplete), which occupy the resultant spaces.

In the Australian Silurian, the family is represented by *Hercophyllum* Jones, remarked below.

Goniophyllum Edwards and Haime (1850, p. lxix) from the Wenlock of England and the Gotlandian of Gotland may be a member of the family, as it has the characteristic septal structure, and an arrangement of horizontal skeletal elements sometimes found in Phaulactids—deeply concave tabular floors. The new Australian genus *Baeophyllum* described herein may be related to *Lamprophyllum*, and it is doubtfully regarded as a member of the Pycnactidae.

Possibly the Entelophyllidae are related to the Pycnactidae, as is suggested in the discussion on p. 411 below.

Genus Hercophyllum Jones.

Jones, 1936, p. 53. *Genotype*, *Cyathophyllum shearsbyi* Sussmilch, 1914, fig. 143. Upper Silurian, Yass district.

Diagnosis.—Large, solitary Rugose corals; the septa are attenuate in the dissepimentarium, but dilated at first in the tabularium, the dilatation decreasing from the axis outwards during ontogeny, with one early reversal; the major septa reach or almost reach the axis, and are gently curved; the tabularium is wide, with gently domed tabular floors, usually of large tabellae; the dissepiments are small and regular, frequently geniculate.

Remarks.—This genus resembles the other Pycnactidae in having the septal dilatation confined to those parts within the tabularium. Jones has considered a difference in the way this dilatation of the septa decreases during the ontogenies of the two genotypes to be of generic value. In *Phaulactis cyathophylloides* the

dilatation decreases from the counter quadrants first, and then gradually towards the cardinal septum; but in *H. shearsbyi* the decrease is general, from the axis outwards, with a reversal (a slight increase) early in ontogeny. These differences are of the same order as those distinguishing Wedekind's five genera, considered above as possible synonyms of *Phaulactis*. Since, however, *H. shearsbyi* has a rather wider tabularium than the European Pycnactidae, and a constant domed arrangement of the large tabellae, it seems convenient to retain *Hercophyllum* as a genus separable from *Phaulactis*, at least until a re-investigation is made of the Gotland specimens, although Lang, Smith and Thomas (1940, p. 67) have regarded them as synonyms.

HERCOPHYLLUM SHEARSBYI (Sussmilch). Plate xii, figs. 8, 9.

Cyathophyllum shearsbyi, nom. nud., Etheridge, 1904, p. 288.—*C. shearsbyi* Sussmilch (ex Etheridge MS.), 1914, fig. 143, facing p. 44. Limestone Ck., Bowning district. Silurian.—*Phaulactis shearsbyi* (Sussmilch), Hill, 1935, p. 507, fig. 18*d*.—*Hercophyllum shearsbyi* (Sussmilch), Jones, 1936, p. 54, Pl. v, figs. 1*a–g*; Pl. vi, figs. 1*a–g*; Pl. vii, figs. 1*h–i*, 2.

Holotype, specimen figured Sussmilch, *loc. cit.*, in Newcastle Technical College Collection.

Diagnosis as for genus.

Remarks.—The species and its ontogeny have been fully described by Jones, *loc. cit.* The diameter may be as great as 50 mm.; there are from 50 to 55 septa of each order in large specimens, the minor being half to two-thirds as long as the major. The species is almost identical morphologically with *Lycophyllum westergardi* Wedekind (1927, p, 72, Pl. 22, figs. 5–7) from the Stricklandinia marls of Visby, which are uppermost Llandovery or lowest Wenlock in age.

I figure on Plate xii, figs. 7*a*, *b*, sections from F 17236 (Australian Museum), in which there is an exceptionally narrow tabularium, in which the axial ends of the major septa are dilated and are continuous vertically, suggesting that the individual belongs to a different species of the genus. As, however, *H. shearsbyi* is exceptionally variable, and this is the only specimen I have showing these characteristics, I refer it provisionally to the group of *H. shearsbyi*. F 12734 and F 17235 (Australian Museum) also show a rather narrow tabularium, but the axial ends of the major septa are thin as in typical adult corallites. All three specimens are from Hatton's Corner.

Localities.—Silurian. Limestone Ck., Bowning; Silverdale; Derrengullen Ck., Bowning; Barrandella shales and Hume Limestone, Hatton's Corner, Yass R.; mouth of Euralie Ck., Yass R.; Quedong, Co. Wellesley; Glenbower anticline, near Boambolo Crossing, Murrumbidgee R.; Spring Ck., near Mt. Canoblas, Co. Ashburnham.

Chapman (1920, p. 183, Pl. 18, fig. 7; Pl. 19, fig. 9) records the species from Native Dog Ck. and Cowombat Ck., Limestone Ck. district, Eastern Victoria, but his figures are inconclusive. The specimen from Wellington (University of Queensland Collection F 3173) referred to by Jones (1936, p. 55), is possibly a species of *Digonophyllum* Vollbrecht (1926) and may be compared with *D. schluteri* Wedekind (Vollbrecht, 1926, Pl. xiv, fig. 4) from the base of the Couvinian of the Eifel.

Genus BAEOPHYLLUM, n. gen.[1]

(*Baeos*, deep, in reference to the tabulae.)

Genotype, *Baeophyllum colligatum*, n. sp., Silurian, Bowspring Limestone, Yass R.

Diagnosis.—Fasciculate Rugose corals with septa partly lamellar, partly of separate trabeculae; with complete or incomplete concave tabulae, and shallow dissepiments.

Remarks.—The relations of this genus are uncertain. The separation of the trabeculae in parts of the septa is known elsewhere only in *Rhizophyllum*. The concave complete and incomplete tabulae are like those of *Disphyllum panicum* (Winchell) from the Middle Devonian of America, but the dissepiments are rather shallow for the Disphyllidae. Both tabulae and dissepiments resemble those of an undescribed species of *Lamprophyllum* Wedekind from the Wenlock limestone of Wenlock Edge, and because of this resemblance the genus is here placed doubtfully with the Pycnactidae. A comparison of *B. colligatum* with other foreign species is given under remarks on the species.

BAEOPHYLLUM COLLIGATUM, n. sp. Plate xii, figs. 10–12.

Holotype, Australian Museum specimen F 9148, with sections AM 704. Silurian, Bowspring Limestone, Boonoo Ponds Ck., Hatton's Corner, Yass R., N.S.W.

Diagnosis.—*Baeophyllum* with connecting processes and with minor septa short or suppressed.

Description.—The corallum is phaceloid, the corallites being connected by processes. The individual corallites are 5 or 6 mm. in average diameter; the maximum diameter is 7 mm., but corallites smaller than 4 mm. are frequent; the type of increase is not known. The major septa extend about two-thirds of the way to the axis, leaving a clear space there; they are about 30 in number in the larger corallites, and are unequally developed, some being lamellar and others consisting wholly or partly of separate trabeculae, whose width is the same as that of the lamellar septum. The minor septa are very short, or, more usually, are suppressed. They also may be of separate trabeculae, or lamellar. The tabularium is about 3 mm. wide. The tabulae are concave, some being complete, but highly inclined, incomplete plates are added to these to form a peripheral series. As seen in transverse sections the intersections of the tabulae are frequently geniculate. The dissepiments are shallow, rather large, horizontally inclined at the periphery, and more steeply inclined in the inner series; usually only two series are developed. The dissepimentarium is seldom more than 1 mm. wide, except where connecting processes occur. The connecting processes are outgrowths of the dissepimentarium from one corallite, which grows till it touches but does not pierce the epitheca of a neighbour.

Remarks.—The separate trabeculae have the appearance of the spines of *Cystiphyllum*. A transverse section figured by Wedekind (1927, Pl. 2, figs. 11, 12) from the Ludlovian of Gotland as *Entelophyllum fasciculatum* Wedekind, somewhat resembles *B. colligatum*, but no vertical section and no description of internal structure is given. The vertical section figured by Lambe (1901, Pl. x, fig. 3) from the Niagaran (Clinton or Lockport) of l'Anse de la Barbe, Quebec, as *Amplexus cingulatus* Billings, is identical with that of our species.

Localities.—In addition to the type locality, the species occurs in the Bowspring limestone at Hatton's Corner, Yass R., and in the limestone at the junction of Euralie Ck. and Yass R. (Por. 161, Parish of Yass). Silurian (Wenlock or Ludlow).

Family RHABDOCYCLIDAE.

Acanthocyclidae, Hill, 1936, p. 193. Typical genus, *Rhabdocyclus* Lang and Smith, 1939, p. 152, nom. nov. for *Acanthocyclus* Dybowski, 1873, preoccupied.

Rugose corals with acanthine septa and complete tabulae, and without dissepiments.

Range.—Silurian and Lower Devonian.

Remarks.—I have included in this family only the Upper Valentian and Wenlock *Palaeocyclus* and *Rhabdocyclus*, the Upper Valentian *Cantrillia* and the Wenlock, Ludlow and Lower Devonian *Tryplasma*. In the three last-named genera, the trabeculae are rhabdacanths or holacanths with the proximal parts embedded in lamellar sclerenchyme which is continuous round the corallum. In *Palaeocyclus* the trabeculae are monacanths. I have considered *Rhabdocyclus* to be directly derived from *Palaeocyclus* by evolution of the trabeculae, and *Tryplasma* to be evolved from *Rhabdocyclus* by the development of tabulae. Bassler (1937), however, has united *Palaeocyclus* and *Rhabdocyclus* with all the other discoid or patellate Rugosa in the Family Palaeocyclidae.

The Mycophyllidae may have arisen from the Rhabdocyclidae. They also are without dissepiments, and have rhabdacanthine septa; but the lamellar sclerenchyme which is present is not continuous round the corallum, that of each septum being separate.

Genus Tryplasma Lonsdale.

Lonsdale, 1845, p. 613.—*Pholidophyllum* Lindstrom, 1870–71, p. 925. Genotype, *Cyathophyllum loveni* Edwards and Haime, 1851, p. 364, Gotlandian of Gotland, which is *Tryplasma*.—*Acanthodes* Dybowski, 1873, p. 364, with five genosyntypes from the Gotlandian of Gotland or the Borkholm beds of Estland, all *Tryplasma* spp.—*Spiniferina* Penecke, 1894, p. 592, nom. nov. for *Acanthodes* Dybowski. Penecke included Lower Devonian *Tryplasma* spp.—*Aphyllostylus* Whiteaves, 1904, p. 113. Genotype, *A. gracilis* Whiteaves, *id.*; for figure see Whiteaves, 1906, Pl. 24, figs. 1, 1*a*. Niagaran of Stonewall, Manitoba.—*Aphyllum* Sochkina, 1937, p. 45, p. 94. Monotype, *A. sociale* Sochkina, *id.*, Pl. vii, figs. 1–4. Wenlock, Eastern slopes of the Urals.—*Tryplasma*, Lang and Smith, 1927, p. 461; Hill, 1936, p. 204.

Genolectotype (chosen Lang and Smith, *loc. cit.*), *Tryplasma aequabile* Lonsdale, 1845, p. 613, 633, Pl. A, figs. 7, 7*a*. Silurian. River Kakva, near Bogoslovsk (east of the Northern Urals).

Diagnosis.—Simple or fasciculate Rugose corals with a narrow peripheral stereozone of rhabdacanthine, holacanthine or dimorphacanthine septa in continuous lamellar sclerenchyme, the trabeculae being free distally; with complete tabulae, and no dissepiments.

Remarks.—The earliest record of *Tryplasma* is from the Borkholm (Upper Ordovician or more probably Valentian) beds of Estland. It is very common in the Gotlandian of Gotland, the Silurian of Russia, the Wenlock and Ludlow of England, the Niagaran of America, the Silurian and Lower Devonian of New South Wales, and the Lower Devonian of Styria, the Eastern Urals, and New South Wales. It is frequently associated with similar fasciculate forms without dissepiments and with complete tabulae, but in which the septa are amplexoid and not acanthine; in the Silurian such forms have usually been called *Pycnostylus*, and in the Devonian, *Amplexus*; they are probably homeomorphic and not related to *Tryplasma*.

Aphyllum sociale Sochkina appears to resemble *Tryplasma rugosum* very closely, with extremely short holacanths for septa, set in a narrow peripheral stereozone.

TRYPLASMA LONSDALEI Etheridge. Plate xii, figs. 13, 14.

Etheridge, 1890, p. 15, Pl. i, figs. 1–6. Silurian, [Hatton's Corner] Yass [R.].—Etheridge, 1907, p. 77, Pl. x; Pl. xi, figs. 2–4; Pl. xii, fig. 1; Pl. xix, fig. 4; Pl. xxv, fig. 5; Pl. xxvi, figs. 1–7; Silurian, Yass District and Wellington District.—? *T. lonsdalei* var. *scalariformis* Etheridge, 1907, p. 80, Pl. xii, figs. 2, 3; Pl. xiv, fig. 4; Pl. xxiv, figs. 7, 8, 8*a*; Pl. xxv, figs. 1–4; Pl. xxvi, figs. 8–10; *partim*. Silurian, Yass, Bowning, Jenolan, Wellington and Molong Districts.—*T. lonsdalei* var. *minor* Etheridge, 1907, p. 81, Pl. xvi, figs. 3, 4; Pl. xxiv, fig. 9; Pl. xxv, figs. 6, 7; Pl. xxvi, fig. 11; *partim*. Silurian, Yass district, i.e. the lectotype, here chosen, F 8502, Australian Museum, Scarp, Yass R., Portion 161, Par. Yass, figured Etheridge, *loc. cit.*, Pl. xxiv, fig. 9, Pl. xxv, fig. 6.—? *T. dendroidea*, Hill, 1937, p. 151, *non T. dendroidea* Etheridge, 1907.

Lectotype (here chosen), F 35512, Australian Museum, Silurian, Hatton's Corner, Yass R., figured Etheridge, 1890, Pl. i, figs. 2–5.

Diagnosis.—Phaceloid *Tryplasma* with corallites 6 mm. in average diameter, with connecting processes.

Description.—The corallum is sub-phaceloid, its long cylindrical corallites diverging very slightly, and the corallum may be more than 150 mm. in height. The corallites are of an average diameter of 6 mm., and are frequently in contact or connected by processes. In some coralla the average diameter may be 8 mm., and in others 4 mm. Increase is axial or peripheral, two, three, or four subequal corallites arising; in axial increase the new corallites may remain in contact for a short distance; but in peripheral increase they usually diverge immediately. The diameter of a corallite increases slightly just before offsets are produced, and at the issue of a connecting process. There are 20 to 30 major septa extending from one-third to half-way to the axis, alternating with an equal number of minor septa which are shorter and thinner than the major septa. Both major and minor septa are acanthine, the distal ends of the trabeculae being free. The trabeculae are rhabdacanths and the width of the peripheral stereozone in which they are set is no greater than the thickness of a major septum. The rhabdacanths of a septum are in contact proximally, and free distally. The tabulae are complete, flat or sagging, sometimes with a median notch. They vary in distance apart from 1 to 2 mm. There are no dissepiments.

Remarks.—Etheridge placed in the variety *scalariforme* specimens from the Molong, Wellington, Jenolan and Nemingha districts, and from Euralie Ck., Boambolo and Limestone Ck. in the Yass district, which had uniformly larger and more parallel corallites, of average diameter 8 mm., in which groups of closely-spaced tabulae were absent, and two, three or four buds occurred, instead of the two considered characteristic of *T. lonsdalei, s.s.* But all these characters are variable in *T. lonsdalei*, and should the specimens showing them possess rhabdacanthine septa, then they are best regarded as *T. lonsdalei*. I have examined those of his syntypes from the Yass district that are at present available, and am unable to find rhabdacanthine septa in them. They appear to have lamellar septa, which would be diagnostic for *Pycnostylus*, but they are all rather re-crystallized, and for the present I place them doubtfully with *T. lonsdalei*. It is considered unwise to choose a lectotype for the variety *scalariforme* until the syntypes from the Molong and Wellington districts have been sectioned.

It seems to me that the individuals placed by Etheridge in *T. lonsdalei* var. *minor* differ from the typical *lonsdalei* only in those characters which are very variable in *lonsdalei*, such as diameter of corallites, spreading nature of the

corallum, and number and position of origin of the offsets in the calice, and that a separation of such forms from *lonsdalei* can neither reasonably nor usefully be maintained.

The specimen described by McCoy (1847, p. 228) from Curradulla or Limestone Ck.* as *Amplexus arundinaceus* Lonsdale, which I previously regarded as *Tryplasma dendroides*, has the rhabdacanthine septa of *T. lonsdalei*, not the amplexoid septa of the lectotype of *Pycnostylus dendroides* which I have since examined. Its diameter is however larger than that found in *T. lonsdalei*.

TRYPLASMA DELICATULUM Etheridge. Plate xii, figs. 17*a*, *b*.

T. delicatula Etheridge, 1907, p. 82, Pl. xxii, fig. 9; Pl. xxiii, figs. 6, 7. Silurian, north bank, Yass R., Por. 126, Par. Yass.—*Lectotype* (here chosen), F 8725, Australian Museum, with slides AM 742, figured Etheridge, *loc. cit.*

Diagnosis.—Phaceloid *Tryplasma* with corallites 1·5 to 3 mm. in diameter, with 15 major and 15 minor septa.

Description.—The corallum is phaceloid, the corallites being long, cylindrical and straight or slightly flexuous, close, united laterally by their walls or by connecting processes. They are from 1·5 to 3 mm. in diameter. The epitheca shows longitudinal ridges and transverse growth striation. The peripheral stereozone is narrow and the holacanthine septa are extremely short (less than 1 mm. long), the major extending a little further beyond the stereozone than the minor. There are usually 15 major septa and 15 minor septa. Holacanths may be developed on the tabulae, which are distant, frequently with a median notch.

Remarks.—The species is close to *T. flexuosum* (Linnaeus) from the Gotlandian of Gotland, and the Wenlock of England, but has slightly more septa, 30 at a diameter of 3 mm. as against 22 at the same diameter in the European form. The other Australian phaceloid *Tryplasma* has almost 40 septa in those few of its corallites which are as small as 3 mm. in diameter, and their septa are rhabdacanthine, not holacanthine.

TRYPLASMA DERRENGULLENENSE Etheridge. Plate xii, fig. 16.

T. derrengullenensis Etheridge, 1907, p. 88, Pl. xxii, figs. 5–8; Silurian, Limestone Ck., near Bowning. *Lectotype* (here chosen), F 9789, Australian Museum, figured Etheridge, *loc. cit.*, fig. 8.

Diagnosis.—Solitary, trochoid or ceratoid *Tryplasma*, with irregular rejuvenescence, and a very deep calice.

Description.—The corallum is solitary, and trochoid at first, later with frequent rejuvenescence so that the various rejuvenescence calices do not exceed the original in diameter, but each grows at an angle from the preceding, and the corallum is irregular. The epitheca shows longitudinal double ridges, the fine furrows opposite the minor septa, and the deeper ones opposite the major septa. The calice is very deep, and bears numerous spines in vertical series, each series representing a septum. Those of the major septa are larger than those of the minor septa. Rootlets may be present. There are about 40 septa of each order at a diameter of 15 mm., the greatest observed in the species. The major septa may be 2 mm. long. The septa are rhabdacanthine, the rhabdacanths being free distally, but having their bases set in lamellar sclerenchyme continuous round the wall, thus forming a peripheral stereozone. The tabulae are complete and

* My reference 1937, p. 151, to the age of the beds in Limestone Ck. as Silurian or Lower Devonian was due to Devonian specimens from Cavan being sent to me wrongly labelled Limestone Ck.

horizontal, sometimes with a median notch. They may be distantly or closely placed in the one corallite, and frequently bear small spines on their upper surfaces.

Remarks.—*T. derrengullenense* is extremely close to and may indeed be synonymous with *Tryplasma loveni* (Edwards and Haime) from the Wenlock of England and the Gotlandian of Gotland. The Australian form is perhaps a little slenderer, with somewhat more irregular rejuvenescence.

Family Spongophyllidae.

Hill, 1939*a*, p. 58.

Range.—Upper Silurian of the Baltic States, Bohemia and New South Wales, Lower Devonian of Styria and France, and Middle Devonian of Europe and Australia.

Genus Spongophyllum Edwards and Haime.

Edwards and Haime, 1851, p. 425; Jones, 1929, p. 88; Hill, 1939*a*, p. 60.—*Genotype* (by monotypy), *Spongophyllum sedgwicki* Edwards and Haime, *loc. cit.*, 1853, p. 242, Pl. lvi, figs. 2, 2*a–e*. [Middle] Devonian [or Frasnian], Torquay.

Diagnosis.—Cerioid Rugose corals in which the tabularium is narrow and the tabulae close and slightly concave, the minor septa are degenerate, and lonsdaleoid dissepiments may be developed in an irregular peripheral zone when the major septa are discontinuous.

Remarks.—The genus as interpreted by Hill, *loc. cit.*, contains five Upper Silurian and six Middle Devonian species.

Spongophyllum shearsbii Chapman. Plate xiii, figs. 1, 2.

Chapman, 1925, p. 113, Pl. xiv, figs. 18*a*, *b*.; Pl. xv, figs. 25, 26. Silurian, Hatton's Corner, Yass R.—Jones, 1932, p. 51, Pl. iii, figs. 1, 2; Pl. iv, fig. 1.

Holotype, specimen, figured by Chapman, *loc. cit.*, in the National Museum, Melbourne.

Diagnosis.—*Spongophyllum* with corallites 5 mm. in diameter, with thick walls; the major septa are long and usually perfect, and the minor septa usually discontinuous; lonsdaleoid dissepiments are rare; tabularium narrow, with complete, sagging tabulae.

Remarks.—The species has been adequately described by Chapman, *loc. cit.*, and Jones, *loc. cit.* Its thick walls and the general absence of lonsdaleoid dissepiments are very characteristic.

Localities.—Bowspring limestone, Hatton's Corner, Yass R., and Boonoo Ponds Ck., near Yass; shales above Bowspring limestone, Hatton's Corner, near Yass. Silurian.

Spongophyllum spongophylloides (Foerste). Plate xiii, figs. 3–5.

Endophyllum (*spongophylloides*?) Foerste, 1888, p. 132, Pl. xiii, figs. 16, 17; coralline limestone, Silurian, Bowning.—*Lonsdaleia*? (*Spongophyllum*) *bipartita* Etheridge, 1889, p. 22, Pl. iii, figs. 1–5; Humewood, near Yass. Silurian.—*Spongophyllum bipartitum* (Etheridge), Chapman, 1925, p. 114.—*S. spongophylloides* (Foerste), Jones, 1932, p. 52, Pl. iii, figs. 3, 4.

Holotype, specimen, figured by Foerste, *loc. cit.*, now in the British Museum (Natural History).

Diagnosis.—*Spongophyllum* with large corallites 10 to 16 mm. in diameter, in which the 18 to 20 major septa and alternating minor septa are withdrawn from

the periphery; with thin walls, a wide lonsdaleoid dissepimentarium, and narrow tabularium with close, complete, sagging tabulae.

Remarks.—Jones (*loc. cit.*) has already given an adequate description, and has noted that, of the described species of *Spongophyllum*, *S. spongophylloides* is closest to the Wenlock (E_2) *S. inficetum* Počta (1902, p. 153, Pl. 102, fig. 1) from Bohemia; but it is larger, has a wider dissepimentarium, and more septa than the Bohemian form.

Localities.—Bowspring and Barrandella limestones, Hatton's Corner, Yass R.; Derrengullen Ck. and Limestone Ck., near Bowning; Bowning; Humewood Lead Mine, near Yass. Silurian.

Genus Yassia Jones.

Jones, 1930, p. 36.—*Crinophyllum* Jones, 1932, p. 61, *nom. nov. inval.*—*Genotype*, *Spongophyllum enorme* Etheridge, 1913, p. 35, Pls. iv–vii; Silurian; escarpment north-east of Boonoo Ponds Ck., Hatton's Corner, Yass R.

Diagnosis.—Cerioid Rugose corals with septa developed only as crests on the dissepiments and tabulae; tabulae complete, shallowly saucered; dissepiments very large, steeply inclined near the axis.

Remarks.—Only the genotype is known; the stability of the tabularium is noteworthy; in most lineages, when the septa are lost, the tabularium merges with the dissepiments, and is hard to distinguish. In *Yassia*, however, the two are quite distinct. The genus is here regarded as a member of the Spongophyllidae in which the loss of the septa is complete. The characters of both dissepiments and tabulae support this classification.

Yassia enormis (Etheridge). Plate xiii, figs. 6*a*, *b*.

Spongophyllum enorme Etheridge, 1913, p. 35, Pls. iv–vii.—*Yassia enormis* (Etheridge), Jones, 1930, p. 36, vide supra.—*Crinophyllum enorme* (Etheridge), Jones, 1932, p. 61, Pl. iv, figs. 2, 3.

Lectotype (here chosen), F 8572, Australian Museum, figured Etheridge, *loc. cit.*, Pl. iv. Silurian, escarpment north-east of Boonoo Ponds Ck., Hatton's Corner, Yass R.

Diagnosis as for genus.

Remarks.—The species has been adequately described by Etheridge, *loc. cit.*, and Jones, *loc. cit.* The corallites are very large, 20 to 40 mm. in diameter, the tabularium occupying nearly one-third of this. Only the type species is known. In addition to the type locality, it occurs in the Bowspring limestone of Hatton's Corner, Yass R.

Family Streptelasmidae.

Hill, 1940, p. 164.

Range.—Upper Ordovician and Silurian of America and Europe; Silurian of Australia; Lower Devonian of France; Middle Devonian of North America and Australia.

Genus Streptelasma Hall.

Streptoplasma [sic] Hall, 1847, pp. 17, 49, 69.—*Streptelasma* Hall, 1847, explanation to Pl. iv.—*Palaeocyathus* Foerste, 1888, p. 129. Genosyntypes, *Turbinolopsis bina* Lonsdale, Phillips, 1841; *Zaphrentis caudata* Ludwig, 1865–6; and *Cyathophyllum australe* Foerste, 1888, p. 128. Genolectotype, chosen Lang, Smith and Thomas, 1940, p. 94, *Cyathophyllum australe* Foerste, described below.—*Streptelasma*, Smith, 1930, p. 311; Cox, 1937, p. 2; Hill, 1940, p. 165.

Genolectotype, *Streptoplasma* (sic) *corniculum* Hall, 1847, p. 69, Pl. 25, figs. 1*a–d*. Trenton formation of Trenton Falls, etc., New York State. See Cox, *loc. cit.*

STREPTELASMA AUSTRALE (Foerste). Plate xii, figs. 18–23.

Cyathophyllum australe Foerste, 1888, p. 128, Pl. xiii, figs. 12–14.

Lectotype (here chosen), R 26519, British Museum (Natural History), figured Foerste, *loc. cit.* Hardened grey-brown shales east of Bowning Hill. Silurian. Collected by John Mitchell.

Diagnosis.—Small trochoid *Streptelasma* in which the axial structure is weak and the septa are straight so that the cardinal fossula is difficult to distinguish.

Description.—The corallum is solitary and broadly or slenderly trochoid, usually slightly curved. The broadest corallite seen had a maximum diameter of 25 mm., attained in a height of 25 mm., and the smallest, a diameter of 8 mm. in a height of 11 mm. The calice is extremely deep, as much as two-thirds the height of the corallum, with a long, sloping border and a flattened axial portion. The epitheca shows weak growth annulation, and very shallow longitudinal furrows corresponding in position with the septa. The cardinal septum is on the longest side of the corallum. There are 20 lamellar septa of each order in the calical border when the maximum diameter of the calice is 10 mm. (Foerste's holotype), and 25 of each order in a transverse section of 10 mm., just below the base of a much wider calice. The septa are straight; they are never attenuate, but are more dilated in the early stages than in the later. The major septa are unequal, reaching almost to the axis; their axial ends may be a little swollen, and those of two neighbours are frequently joined. They are denticulate, so that a weak axial structure is formed, which is distinct enough in vertical section, but not very obvious in transverse section. It is difficult or impossible to distinguish either cardinal septum or cardinal fossula from the arrangement of the septa. The minor septa are very short, and are dilated to form a peripheral stereozone 0·5 to 1 mm. wide, with the dilated peripheral ends of the major septa. The tabulae are distant, complete and domed, broken by the septa and their denticulations.

Remarks.—The holotype of *Cyathophyllum australe* Foerste is a specimen difficult to interpret (H. D. Thomas *in litteris*). It appears to be partly calical mould and partly solid, affected by weathering. It is unsuitable for sectioning, but its septa are lamellar, not acanthine, rather long, extending well towards the axis. It seemed very likely that the specimens from Rainbow Hill and Bellevale (Phacops bed) used for the diagnosis and description given above, are conspecific with it. I sent specimens to Dr. Thomas to be compared with the type, and he reports that in his opinion they are conspecific. It may be that two species are present in the trochoid coralla of the Phacops bed. In two specimens, the lumen is almost completely filled with sclerenchyme, apparently by dilatation of the septa. However, Smith (1930, p. 312) has described similar great dilatation in the young stages of a Valentian Streptelasmid, and it may be that these two specimens are of the same species as the others, but still retain in the adult stage thickening which in the others died away very early. The number and arrangement of the septa correspond fairly well, 27 as against 25 major septa at a diameter of 10 mm., but it is not clear whether their axial edges are denticulate.

Family ENTELOPHYLLIDAE.

Typical Genus, *Entelophyllum* Wedekind.

Compound Rugose corals with long major septa typically ending at a loose axial structure of incomplete tabulae, and with numerous small, globose dissepiments.

Range.—Gotlandian of Gotland and Oesel, Upper Silurian of Norway, ? Llandovery, Wenlock and Ludlow of England, Wenlock of Scotland, Wenlock of Bohemia, Niagaran of America and Upper Silurian of Australia.

Remarks.—The following genera may be related to *Entelophyllum*:

Petrozium Smith (1930, Pl. xxvi, figs. 20–28) from the Upper Llandovery of England is a small phaceloid form with long septa, globose dissepiments, and tabulae arranged in an axial structure. It may well be a member of the family.

Weissermelia Lang, Smith and Thomas (1940, p. 111), nom. nov. for *Ptilophyllum* Smith and Tremberth (1927, p. 309), preoccupied, from the Ludlow of Gotland is fasciculate, with carinate septa, but the incomplete tabulae are arranged in concave platforms: it also has rather larger dissepiments than typical *Entelophyllum* though from the figures these seem to resemble the peripheral dissepiments of the Australian Upper Silurian *E. yassense* and the American Niagaran *E. rugosum*.

Cyphophyllum Wedekind (1927, p. 20) from the Wenlock of Gotland, contains solitary corals with the axial structure and septal arrangement of *Entelophyllum*, but the septa are frequently discontinuous with the occurrence of lonsdaleoid dissepiments. The genus is probably a member of the Entelophyllidae.

Phaulactis near *angusta* Lonsdale (Smith, 1930, Pl. xxvii, figs. 1–4) is a solitary coral from the Upper Llandovery of England, which, from the arrangement of its tabulae, appears to have closer relation to *Entelophyllum* than to *Phaulactis*.

Lang and Smith (1927, p. 457) considered that *Entelophyllum* gave rise to *Codonophyllum* Wedekind by septal dilatation, so that *Codonophyllum* might perhaps be regarded as a member of the family. It is not impossible that the Entelophyllidae are related to the Pycnactidae, and that they might be regarded as a sub-family of the latter. The chief difference is in the nature of the dilatation of the septa. In the Entelophyllidae this affects the septa in the dissepimentarium, but in the Pycnactidae those parts in the tabularium are the ones dilated.

Genus Entelophyllum Wedekind.

Wedekind, 1927, p. 22.—*Xylodes* Lang and Smith, 1927, p. 461; Smith and Tremberth, 1929, p. 362; Smith, 1933, p. 513, genotype by designation, *Madreporites articulatus* Wahlenberg. *Xylodes* is pre-occupied by Waterhouse, 1876, for a recent coleopteron.

Genolectotype (chosen Lang, Smith and Thomas, 1940, p. 57): *Entelophyllum articulatum* Wedekind, 1927, pp. 22, 24 = *Xylodes articulatus* (Wahlenberg) Smith and Tremberth, 1929, p. 363, Pl. vii = *Madreporites articulatus* Wahlenberg. Upper Silurian, Gotland.

Diagnosis.—Compound Rugose corals typically with peripheral parricidal increase, long thin septa of which the major reach, or nearly reach, the axis, an axial structure of axial tabellae surrounded by concave periaxial tabellae, and numerous, small, globose dissepiments.

Remarks.—European species are three—the genotype, with attenuate septa, from the Wenlock and Ludlow of England and the Wenlock of Bohemia in addition to the type locality; *Entelophyllum pseudodianthum* (Weissermel), with carinate, dilated septa, from the Wenlock, both having the typical axial structure, and a cerioid species from the Upper Silurian of Norway (Smith and Tremberth, 1929, Pl. viii, fig. 1). The American Niagaran species, *E. rugosum* (Smith) (1933,

p. 516) has complete tabulae and no axial structure, and a peripheral series of rhombic dissepiments. The Australian Silurian *E. yassense* (Etheridge) has a peripheral series of rhombic dissepiments, and an axial structure. The internal structure of the Australian *E. latum*, n. sp. is very similar to that of the genotype. I have seen a cerioid form from Bungonia, New South Wales.

ENTELOPHYLLUM YASSENSE (Etheridge). Plate xiii, figs. 11, 12.

Heliophyllum yassense Etheridge, 1892, p. 170, Pl. xi, fig. 8, Pl. xii, figs. 1–3. [Silurian] Near Yass.—*Xylodes yassense* (Eth. fil), Jones, 1936, p. 56, Pl. vii, figs. 3, 4, possibly *non* fig. 5.

Type material missing, possibly in Geological Survey of N.S.W. collection.

Diagnosis.—Entelophyllum with carinate septa, minor septa withdrawn from the inner margin of the dissepimentarium, and with a peripheral series of rhomboid dissepiments.

Description.—The corallum is fasciculate, spreading in a wide cone from the first corallite, increase being peripheral and unequal, the larger part of the parent corallite being unaffected and continuing with the growth of the parental tabularium; this non-parricidal peripheral increase may perhaps better be regarded as a modification of lateral increase. The coralla may be very large, one observed in Limestone Creek being several feet in height and diameter. The size of the corallites is very variable, from long sub-cylindrical to short, broadly trochoid. The broadest individual corallite observed was 50 mm. in diameter, the longest 80 mm. in height; usually, however, increase takes place before such a size is attained. Owing to the nature of the increase the corallites are frequently sinuously oval in transverse section. The calice has a broad, flat platform, and a shallow axial pit in which four fossulae may be distinguished, just outside the axis, one, the cardinal, being much deeper.

There are two orders of attenuate septa, both carinate, the carinae being lateral outgrowths from the trabeculae, irregularly arranged on either side of the septa, running parallel to the trabeculae—i.e., upwards, curving inwards. The septa in the larger corallites are very crowded—in the corallite 50 mm. in diameter more than 200 septa were counted; in another of 30 mm. diameter, there were 126; 30 were present in a corallite of 6 mm. diameter. In most corallites the septa are straight for a distance of 1 mm. from the epitheca, i.e. opposite the outermost series of dissepiments; inside this they are rather sinuous. The major septa are very long, extending almost to the axis, but leaving there a space about 2 mm. in diameter, into which usually two opposite longer septa, the counter and the cardinal, project. Near their axial edges the two major septa neighbouring the cardinal septum are slightly curved, outlining a small fossula in the tabularium. The minor septa seldom extend the full width of the dissepimentarium; they are unequal; their axial ends may curve towards the neighbouring major septum on the counter side. The tabulae are arranged in axial and periaxial series of incomplete plates; the periaxial series is of slightly saucered plates; the axial series forms a loose axial structure, the outermost plates being globose and the inner flattened or sagging. The width of the tabularium varies with the width of the corallite, from 6 to 10 mm. The dissepiments are in two distinct groups—the peripheral group of one or two series is of rhomboid dissepiments—with a long horizontal or slightly inclined peripheral part (as seen in vertical section) and a globosely curved inner part. In transverse section these plates are geniculate. The inner group of dissepiments occupies the rest of the

dissepimentarium, which in large corallites may be very wide; they are typically small, globose and slightly inclined; but occasionally the place of several may be taken by a single, long, shallow, gently inclined plate.

Remarks.—This species differs from the Wenlock and Ludlow English and Baltic *E. articulatum* and *E. pseudodianthum* in the nature of the increase, for the tabularium of the parent continues as the tabularium of the largest product; while in the European forms the increase is parricidal. *E. yassense* also has a peripheral series of rhomboid dissepiments, unknown in the European forms, but which, from the figures given by Smith (1933, Pl. i, figs. 8–11) appears to occur in the American Niagaran *E. rugosum*; it differs from *E. rugosum* in that its tabulae form an axial structure, while in *E. rugosum* the tabulae are usually complete and horizontal. Its septa are carinate as in *E. pseudodianthum*. It differs from the forms placed in the Gotlandian *Cyphophyllum* by Wedekind in not having lonsdaleoid dissepiments. As the species does not resemble very closely any other known member of the genus, its age can only be deduced as between the known limits of occurrence of the genus, Wenlock and Ludlow of Europe and Niagaran of America.

Localities.—Hatton's Corner, Yass R., in the Barrandella shales and the Hume limestone. Derrengullen Ck., Silverdale, Barber's and Limestone Cks., near Bowning. Rainbow Hill, near Yass. Silurian.

ENTELOPHYLLUM YASSENSE var. PATULUM (Foerste). Plate xiii, figs. 13*a*, *b*.

Cyathophyllum patula Foerste, 1888, p. 129, Pl. xiii, figs. 9–11. Lower trilobite bed, Bowning. Silurian.

Type material untraced, possibly in the British Museum.

Diagnosis.—Patellate *E. yassense*, solitary, or increasing once only, by peripheral increase.

Description.—The corallites are patellate and vary in dimensions; one was 10 mm. tall, 35 mm. broad in one diameter, and 29 mm. broad at right angles to this; another was 8 mm. tall, and 42 × 34 mm. in diameter. The apex is excentric, so that the corallites are slightly curved. They are usually solitary, but one was observed in which an offset was produced by parricidal peripheral increase from the parent. In calical characters and internal structure the variety resembles *E. yassense*.

Remarks.—This variety occurs in beds higher in the succession than the species; its typically solitary mode of growth, and the fact that when increase occurs it is parricidal, distinguish it from the earlier species. It may be that it should be regarded not as a variety but as a forma, but since *patula* was an earlier name than *yassensis*, this would make taxonomic difficulties; and as *patula* appears to have a stratigraphical value, it is herein regarded as a variety.

Localities.—In addition to the type locality, the variety occurs in the Hume limestone of Hatton's Corner, Yass R. Silurian.

ENTELOPHYLLUM LATUM, n. sp. Plate xiii, figs. 8–10.

Holotype, F 8973, Australian Museum Collection, collected by Shearsby, 1903, from the Silurian anticline at Glenbower, near the Boambolo crossing of the Murrumbidgee River, N.S.W. There is a second specimen from the same locality, F 8974, and three others, F 9548–9550, from the contorted shales west of the crossing, collected by Shearsby, 1904.

Diagnosis.—*Entelophyllum* with numerous thin septa and with axial structure so wide as almost to fill the tabularium.

Description.—Only broken individuals have been collected, so that it is not known whether the corallum is phaceloid or solitary. They vary in diameter from 12 to 20 mm., and appear to be slowly expanding. At a diameter of 18 mm. there are 40 major and 40 minor septa, both thin and closely-spaced, the minor septa extending a little beyond half-way to the axis, and the major continuing to or almost to the axis, with more or less rotation noticeable. In the tabularium the tabellae are arranged in a wide axial structure in which there is a circumferential series of plates which are domed and horizontally based, separated from the dissepimentarium by small plates inclined outwards, and surrounding wide plates which are shallowly concave. The dissepiments are very small, regular and rather globose.

Remarks.—The specimens from the contorted shales show septa thickened and with carinae, while those from the anticline have smooth, thin septa. The species is close to *Entelophyllum articulatum* (Wahlenberg) from the Wenlock and Ludlow of Europe, differing in having more septa and a wider axial structure.

RUGOSA INCERTAE SEDIS.

Genus ZENOPHILA, n. gen.

(*Zenophila*, a heroine in the poems of Meleager.)

Genotype, *Phillipsastraea walli* Etheridge. Silurian, Yass District.

Diagnosis.—Plocoid Rugose corals with small, distant tabularia surrounded by an aureole of regularly radial septal segments; with horizontal or concave tabulae, and shallowly arched dissepiments.

Remarks.—The genus, which contains only the type species, bears a superficial resemblance to the only other figured Silurian plocoid genus, *Arachniophyllum* Dana, which is characteristic of the Wenlock Limestone of England, the Niagaran of America and the Silurian of Gotland. *Arachniophyllum*, however, always shows a peculiar septal modification, by which at recurrent levels in the corallum the septa are represented in the dissepimentarium by a rectilinear network continuous over the surfaces of the dissepiments (see Lang and Smith, 1927, p. 453). It also has an axial structure, where the axial edges of the septa meet the conically arranged tabellae. *Zenophila* shows no trace either of this septal modification or of an axial structure. *Phillipsastraea silurica* Lahusen (Weissermel, 1894, p. 611) from the Upper Silurian of Estland is not sufficiently known for a comparison to be made with it; when Etheridge wrote, all plocoid corals of any Palaeozoic period were placed in *Phillipsastraea*. *Z. walli*, however, has none of the characteristics of the Disphyllidae, to which *Phillipsastraea*, *s.s.* belongs. It has shallowly arched dissepiments, in contrast to the rather globose plates of the Disphyllidae, it shows none of the septal modifications of the Disphyllidae, and its tabularium is not of a type known in the Disphyllidae. I know of no genus which might be considered related to *Zenophila*.

ZENOPHILA WALLI (Etheridge). Plate xiii, figs. 14–17.

Phillipsastraea walli Etheridge, 1892, p. 169, Pl. xi, fig. 7, Silurian, Yass district.—*non P. walli*, Chapman, 1914, p. 305, Pl. xlviii, figs. 7–9, Lower Devonian, Loyola, which (Hill, 1939, p. 238) is *Phillipsastraea* sp. indet.

Type material missing, possibly in Geological Survey of N.S.W. collection.

Diagnosis.—*Zenophila* with dissepimental platforms sagging between the tabularia, and a series of horizontally based dissepiments near the inner margin of the dissepimentarium.

Description.—The corallum is plocoid and spreading, and may be large, one incomplete specimen being 20 × 18 × 7 cm. Neighbouring corallites are never separated by a dividing wall; they are either thamnastraeoid (when the septa of neighbouring corallites are confluent) or aphroid (when the peripheral parts of the septa have not been developed and the corallites are joined by dissepiments only). Th axes oi the corallites are usually from 5 to 10 mm. apart, not very regularly spaced. There are 10 to 12 major septa, extending nearly to the axis; one may be longer than the others; or sometimes a second and nearly opposite septum may also be very long. Minor septa are imperfectly continuous, occurring as crests or segments of variable length; some may be quite absent in any corallite —but in such a case the remaining septa are arranged so that all interseptal loculi are approximately equal. The major septa are always quite straight and radial at the junction between the tabularia and dissepimentaria, but outside this zone they may curve suddenly or gradually, to become confluent with septa from neighbouring corallites, or they may not be formed at all, so that the corallum is aphroid. In some coralla all the septa are attenuate; in others they may be dilated; and in one they are represented, in a fairly narrow zone round the tabularia, by discontinuous trabeculae about 0·05 mm. in diameter, set in a scanty cloudy mass of sclerenchyme; the trabeculae however are not arranged in a rectangular pattern as in *Arachniophyllum*; they appear to be in rows parallel to the course of the septum, but no rows can be seen normal to these, as is characteristic of *Arachniophyllum*. The tabulae are complete, and either sagging or horizontal; the dissepiments are rather flatly curved; the innermost series is highly inclined, but immediately around this is a zone of horizontally based plates; outside this again, the dissepiments are arranged in a sagging curve, the deepest part of the sag being at the approximate junction of two corallites.

Remarks.—The species is known only from the Silurian of Yass and Bowning districts, from the Barrandella shales and Hume limestone of Hatton's Corner, Yass R., the Scarp, Yass R., north bank, Por. 126, Par. Yass, and from Limestone and Derrengullen Cks.

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EXPLANATION OF PLATES XI-XIII.

Plate xi.

Figures × 1·5 approx., except otherwise indicated.

Fig. 1.—*Pycnostylus guelphensis* Whiteaves. Section of topotype, F 3458, University of Queensland Collection; Guelph (? Lower Ludlow), Hespeler, Ontario.

Fig. 2.—*Pycnostylus congregationis* (Etheridge). Syntype, F 8768, Australian Museum Collection; Silurian, Barber's Ck., off Derrengullen Ck., near Bowning, N.S.W. 2*a*, transverse section, AM 732; 2*b*, vertical section, AM 650.

Fig. 3.—*Pycnostylus dendroides* (Etheridge). Transverse section (AM 649) of syntype F 8898, Australian Museum Collection.

Figs. 4-10.—*Rhizophyllum interpunctatum* de Koninck. 4, External view of calical mould, × ¾; F 4279, University of Queensland Collection, Yass R. Silurian.—5, Transverse section, Sydney University Collection; Silurian, Barrandella shales, Hatton's Corner, Yass R.—6, Transverse section, Sydney University Collection; Silurian, Barrandella shales, Hatton's Corner, Yass R.—7, Transverse section, F 3822, University of Queensland Collection, Barrandella shales, Silurian, Hatton's Corner, Yass R.—8, Vertical section, F 3823, University of Queensland Collection, Silurian, Barrandella shales, Hatton's Corner, Yass R.—9, Vertical section, Sydney University Collection, Silurian, Barrandella shales, Hatton's Corner, Yass R.—10, Tangential vertical section, Sydney University Collection, Silurian, Barrandella shales, Hatton's Corner, Yass R.

Fig. 11.—*Rhizophyllum robustum* Shearsby. Sections from F 26872, Australian Museum Collection, Silurian, Limestone Ck., near Bowning; *a*, transverse, *b*, vertical.

Fig. 12.—*Rhizophyllum yassense* Shearsby. External views, approximately × ¾, of the holotype, F 37055, Australian Museum Collection, Silurian, shales in Derrengullen Ck. at the junction with Limestone Ck., near Bowning; *a*, side; *b*, calical, showing the crescentic opening.

Fig. 13.—*Cystiphyllum* sp. cf. *bohemicum* Pocta. Sections from F 3554, University of Queensland Collection, Silurian, Bowspring Limestone, Hatton's Corner, Yass R. *a*, transverse; *b*, vertical.

Fig. 14.—*Holmophyllum multiseptatum*, n. sp. Sections from the holotype, F 1023, University of Queensland Collection, Cliftonwood, near Yass, Silurian. *a*, transverse; *b*, vertical.

Figs. 15-17.—*Disphyllum praecox*, n. sp. 15, Sections AM 744 from F 9719 (Australian Museum Collection); Silurian, Por. 161, Par. Yass (Station 108, Yass R.), N.S.W. *a*, transverse; *b*, vertical.—16, Sections AM 745 from F 9709, the holotype, Australian Museum Collection; Silurian, shale in Limestone Ck., 50 yards below the Bowning-Wargeila road crossing. *a*, transverse; *b*, vertical.—17, Sections from F 9879, Australian Museum Collection; Silurian, Limestone Ck., Bowning District.

Figs. 18-19.—*Mycophyllum liliiforme* (Etheridge). 18, Transverse section from near base of cup, 6184, Sydney University Collection; Silurian, Bowspring Limestone, Derrengullen Ck., Yass. See Pl. xii, fig. 6*b*.—19, Tangential section through septa of cup, F 3810, University of Queensland Collection; Silurian, Derrengullen Ck., Yass.

Plate xii.

Figures × 1·5 approx., unless otherwise indicated.

Figs. 1-2.—*Mycophyllum crateroides* (Etheridge). 1, External view, F 8296, Australian Museum Collection; Silurian, Hatton's Corner, Yass R. × slightly less than ¾.—2, Vertical section AM 797 from F 5170, Australian Museum Collection; Silurian, Yass.

Figs. 3-6.—*Mycophyllum liliiforme* (Etheridge). 3, Surface of vertical cut through F 3808, University of Queensland Collection; Silurian, Derrengullen Ck., Yass R.; shows at the top a section through a possible operculum. × ¾.—4, Surface of vertical cut through a typically patellate calice, 6180, Sydney University Collection; Silurian, Hatton's Corner, Yass R. The thinness of the calical wall distinguishes the species from *crateroides*. A young corallite is sectioned on each calical wall. × less than ¾.—5, Vertical section AM645 from F 8896, Australian Museum Collection; Silurian, Barber's Ck., off Derrengullen Ck., Yass R.—6*a*, Transverse section through a fragment, 6183, Sydney University Collection, which may be stem of *M. liliiforme*, or *Pycnostylus* sp.; Bowspring Limestone, Derrengullen Ck., Yass R.—6*b*, Vertical section through a fragment, 6184, Sydney University Collection, which may be stem of *M. liliiforme*, or *Pycnostylus* sp. Bowspring Limestone, Derrengullen Ck., Yass R. See Pl. xi, fig. 18.

Fig. 7.—*Hercophyllum* aff. *shearsbyi* (Sussmilch). Sections from F 17236, Australian Museum Collection; Silurian, Hatton's Corner, Yass R. *a*, transverse; *b*, vertical.

Figs. 8-9.—*Hercophyllum shearsbyi* (Sussmilch). 8, Transverse section, F 4200, University of Queensland Collection; Silurian, Hatton's Corner, Yass R.—9, Vertical section, F 4203, University of Queensland Collection; the broken line shows the probable unweathered outline; Silurian, Hatton's Corner, Yass R.

Figs. 10-12.—*Baeophyllum colligatum*, n. gen. et sp. 10, Sections from F 3779, University of Queensland Collection; Silurian, Derrengullen Ck., Yass R. *a*, transverse; *b*, vertical.—11, Vertical section AM 625, from F 8642, Australian Museum Collection; Silurian, Limestone at mouth of Euralie Ck., Por. 161, Par. Yass (Station 108, Yass R.).—12, Sections AM 704 from the holotype, F 9148, Australian Museum Collection; Silurian,

Bowspring Limestone, Boonoo Ponds Ck., near Hatton's Corner, Yass R. *a*, transverse; *b*, *c*, vertical.

Figs. 13-15.—*Tryplasma lonsdalei* Etheridge. 13, Sections from F 3851, University of Queensland Collection; Silurian, Derrengullen Ck., Yass R. *a*, transverse; *b*, *c*, vertical.—14, Vertical section AM 600 from syntype F 8502, Australian Museum Collection; Silurian, NE bank of Yass R., Por. 126, Par. Yass (Station 106, Yass R.).—15, Sections AM 726 from syntype F 8643, Australian Museum Collection, of *T. lonsdalei* var. *scalariforme* Etheridge. It is impossible to decide from this section whether the specimen is *Tryplasma* or *Pycnostylus*, owing to excessive recrystallization. Silurian, Limestone at mouth of Euralie Ck., Yass R.

Fig. 16.—*Tryplasma derrengullenense* Etheridge. External views, polished transverse surface, F 9793, and polished tangential surface, F 9794, Australian Museum Collection; Silurian, Limestone Ck., Bowning. × ¾. Note vertical rows of dots representing septal spines.

Fig. 17.—*Tryplasma delicatulum* Etheridge. Sections AM 742 of the lectotype F 8725, Australian Museum Collection; Silurian, north bank of Yass R., Por. 126, Par. Yass (Station 106, Yass R.). *a*, transverse; *b*, vertical.

Figs. 18-23.—*Streptelasma australe* (Foerste). 18, External view of the lectotype R 26519, British Museum (Natural History); Silurian, hardened grey-brown shales east of Bowning Hill, Coll. J. Mitchell. The specimen is in part calical cast and in part skeleton.—19, Vertical section of F 3530, University of Queensland Collection; Silurian, Phacops beds, Rainbow Hill, Yass.—20, Transverse section of F 3523, University of Queensland Collection; Silurian, Phacops beds, Rainbow Hill, Yass.—21, Transverse sections from thickened specimen, F 3531, University of Queensland Collection; Silurian, Dalmanites bed, Bellevale, near Yass.—22, Transverse sections from F 3533, University of Queensland Collection; Silurian, Dalmanites bed, Bellevale.—23, Transverse section through the calice of F 3534, University of Queensland Collection; Silurian, Dalmanites bed, Bellevale.

Plate xiii.

Figures × 1·5 approx. unless otherwise indicated.

Figs. 1-2.—*Spongophyllum shearsbii* Chapman. 1, Transverse section of F 3838, University of Queensland Collection; Silurian, Derrengullen Ck., Yass, N.S.W.—2, Vertical section F 3837, University of Queensland Collection; Silurian, Bowspring Limestone, Hatton's Corner, Yass R.

Figs. 3-5.—*Spongophyllum spongophylloides* (Foerste). 3, Transverse section F 3842, University of Queensland Collection; Silurian, Derrengullen Ck., Yass R.—4, Transverse section F 3841, University of Queensland Collection; Silurian, Derrengullen Ck., Yass R.—5, Vertical section of F 3651, University of Queensland Collection; Silurian, Barrandella Limestone, Hatton's Corner, Yass R.

Fig. 6.—*Yassia enormis* (Etheridge). Sections from F 1046, University of Queensland Collection; Silurian, Bowspring Limestone, Hatton's Corner, Yass R. *a*, transverse; *b*, vertical.

Figs. 8-10.—*Entelophyllum latum*, n. sp. 8, Transverse section from F 9549, Australian Museum Collection; Silurian, contorted shales west of Boambolo Crossing, Murrumbidgee R., N.S.W.—9, Vertical section from F 9550, Australian Museum Collection; Silurian, contorted shales west of Boambolo Crossing, Murrumbidgee R., N.S.W.—10, Sections from the holotype F 8973, Australian Museum Collection; Silurian, anticline near Boambolo Crossing, west bank, Murrumbidgee R. *a*, transverse; *b*, vertical.

Figs. 11-12.—*Entelophyllum yassense* (Etheridge). 11, Sections, AM 677 from F 8846, Australian Museum Collection; Silurian, Barber's Ck., Derrengullen Ck., near Bowning. *a*, transverse; *b*, vertical.—12, Sections from F 15917, Australian Museum Collection; Silurian, shale below limestone, Rainbow Hill, near Yass. *a*, transverse; *b*, vertical.

Fig. 13.—*Entelophyllum yassense* var. *patulum* (Foerste). External views of F 9778, Australian Museum Collection; Silurian, Limestone Ck., near Bowning, N.S.W. *a*, proximal; *b*, distal; the match and shadow indicate how patellate the corallite is. Approx. × ¾.

Figs. 14-17.—*Zenophila walli* (Etheridge). 14, Transverse section of F 3877, University of Queensland Collection; Silurian, Derrengullen Ck., Bowning district.—15, Sections from F 6694 (Geological Survey of N.S.W.) now in Australian Museum Collection; Silurian, Derrengullen Ck. *a*, transverse; *b*, vertical.—16, Sections from F 463, Australian Museum Collection; Silurian, Yass. *a*, transverse; *b*, vertical.—17, Transverse section from F 3876, University of Queensland Collection; Silurian, Derrengullen Ck.

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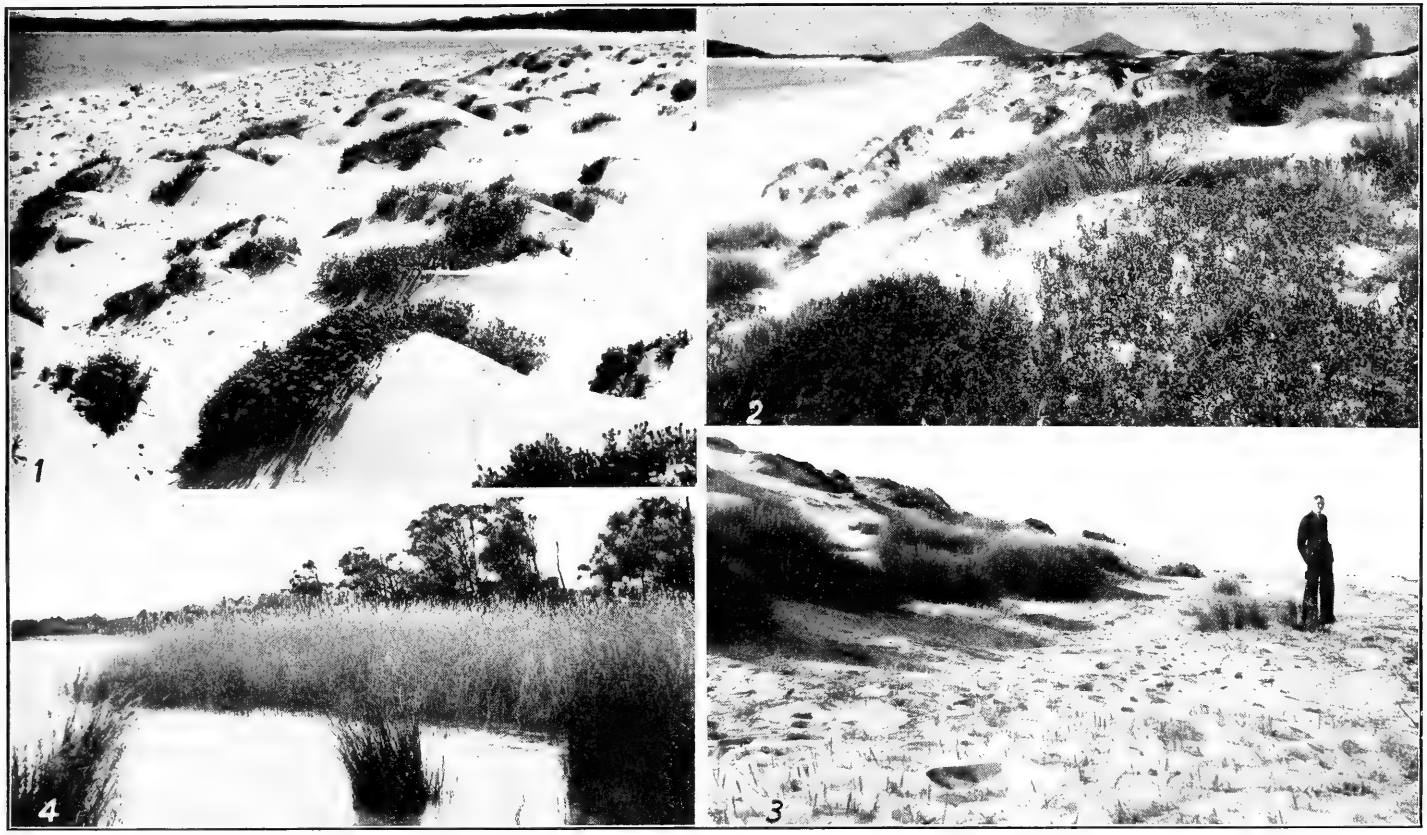

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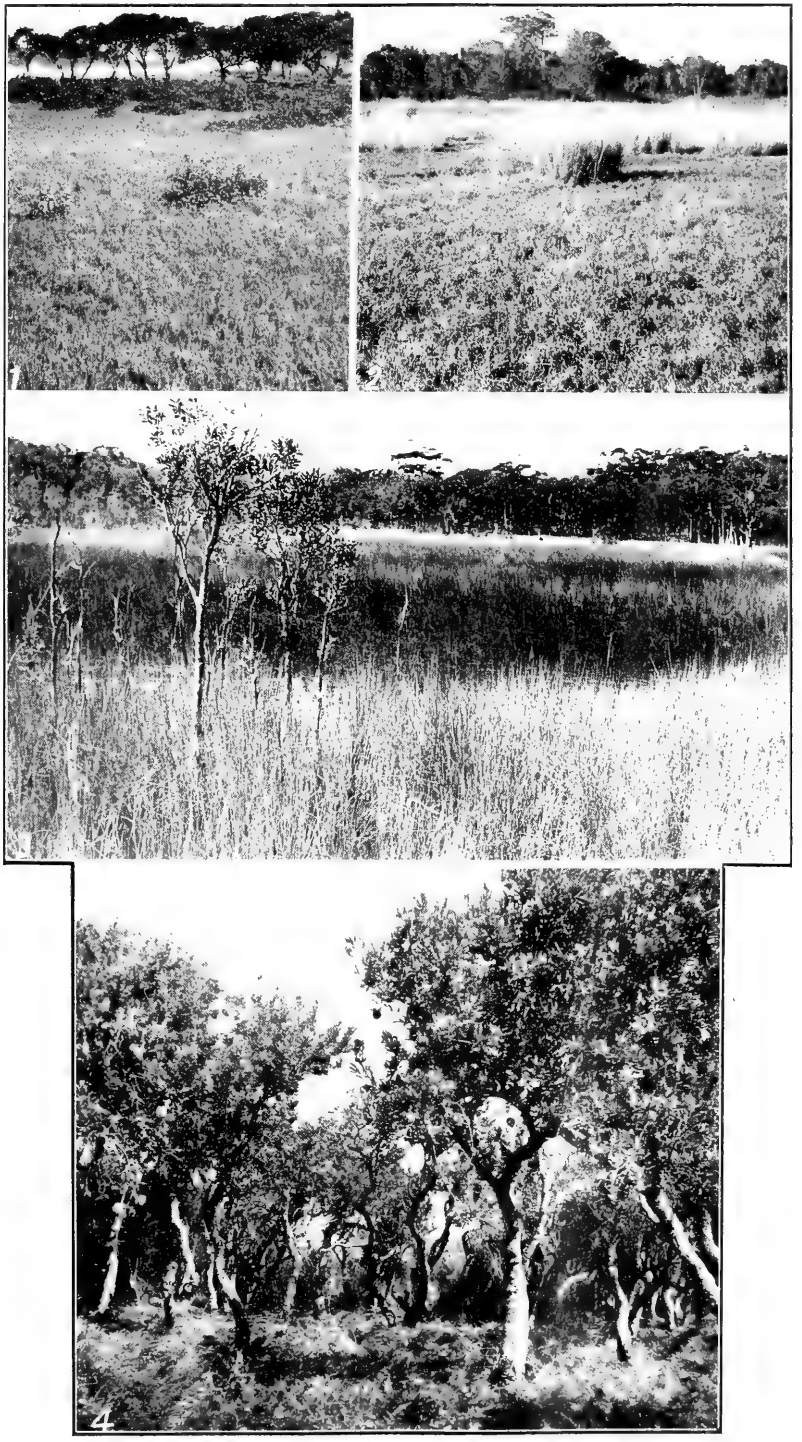

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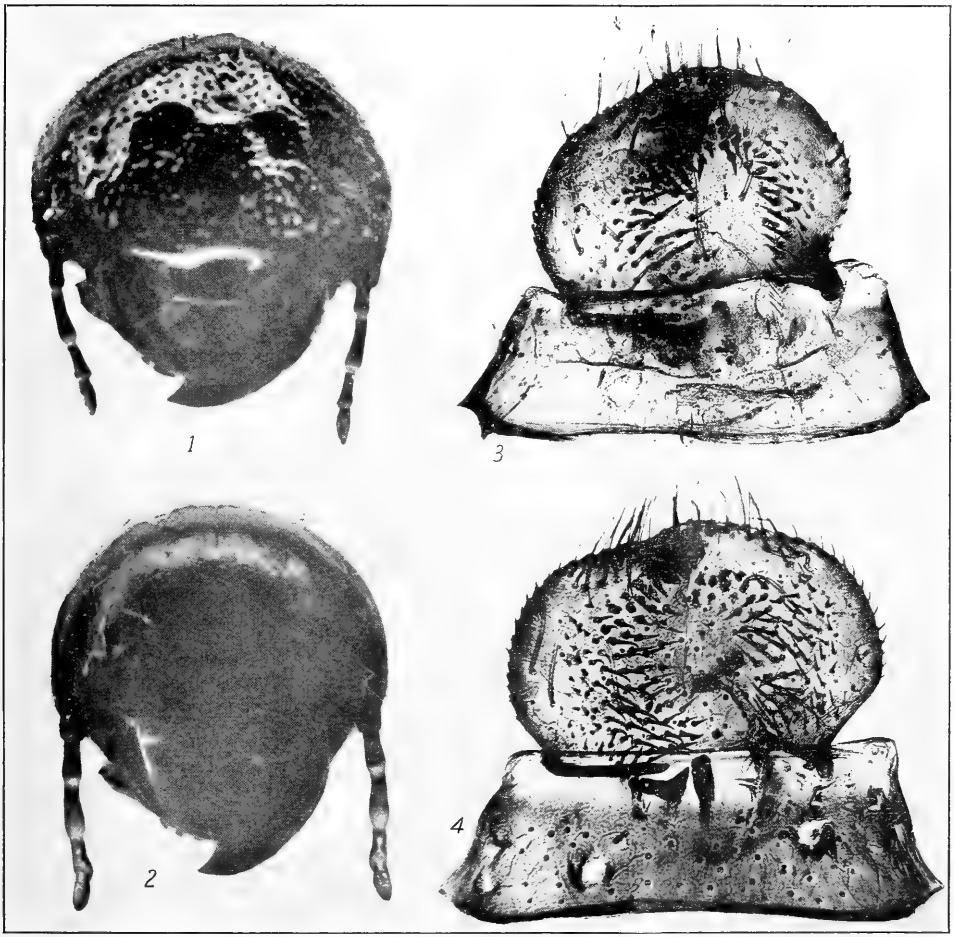
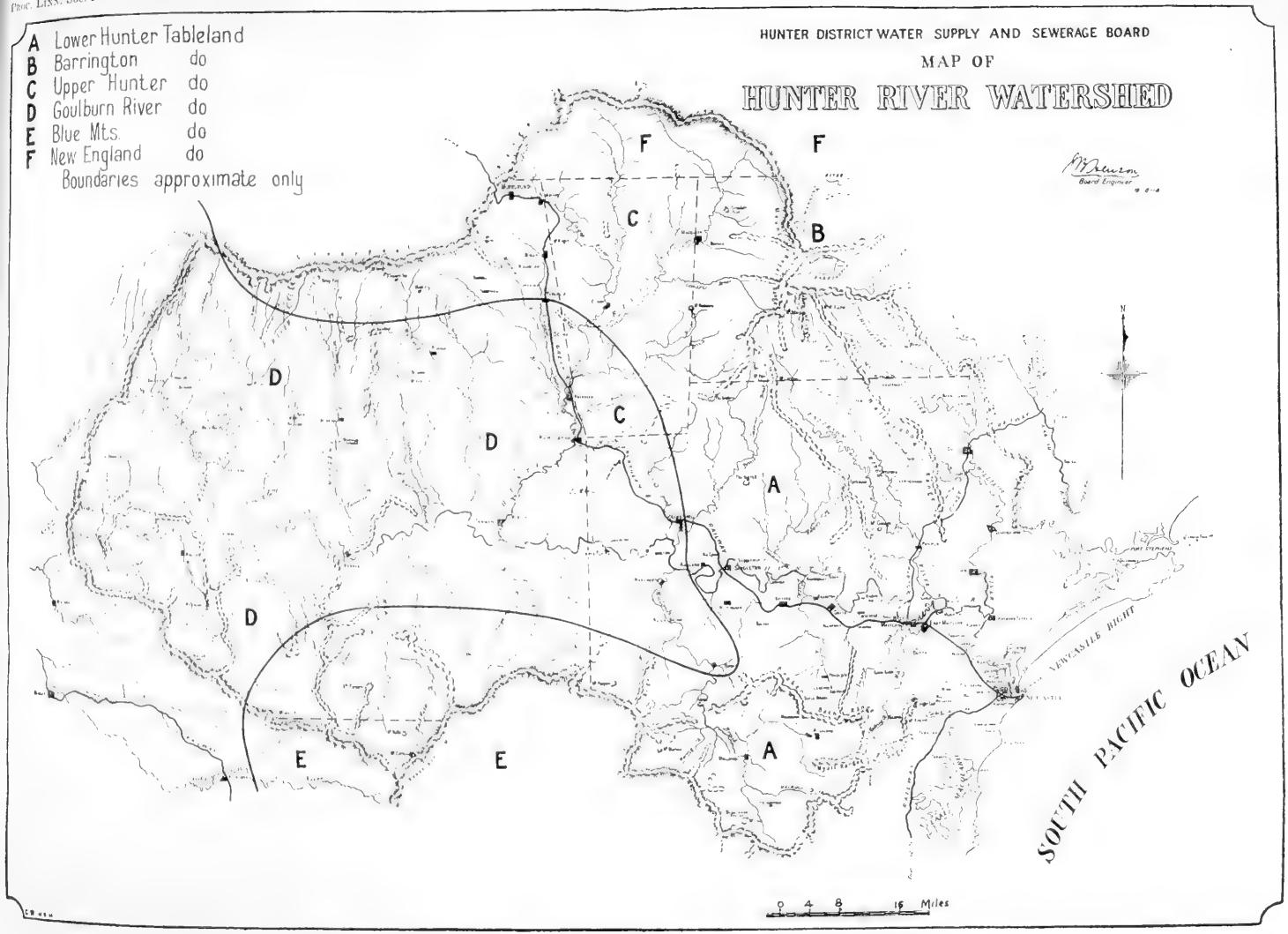


1, 4.—*Metanastes vulgivagus.* 2, 3.—*Heteronychus sanctae-helenae.*


A Lower Hunter Tableland
B Barrington do
C Upper Hunter do
D Goulburn River do
E Blue Mts. do
F New England do
Boundaries approximate only
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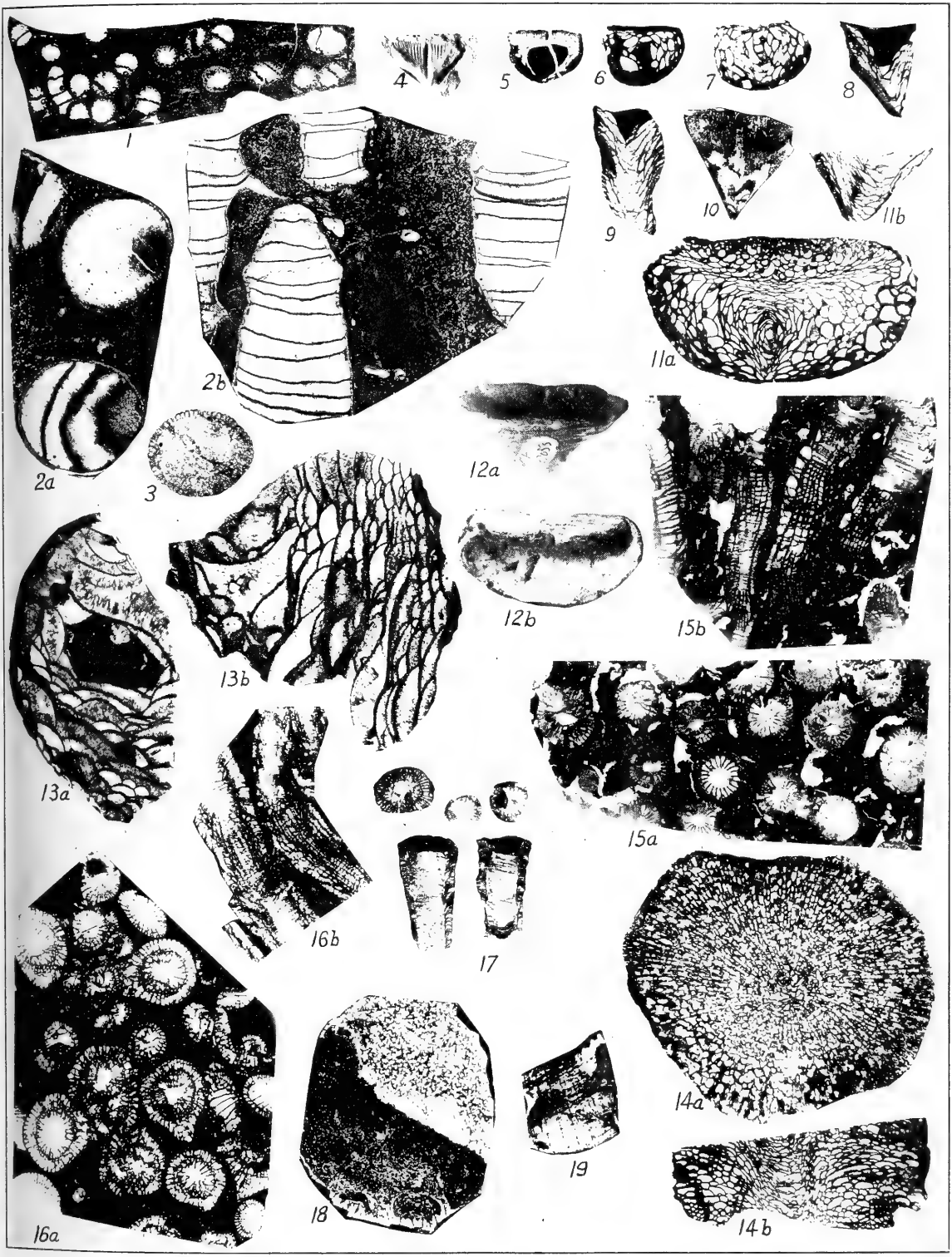
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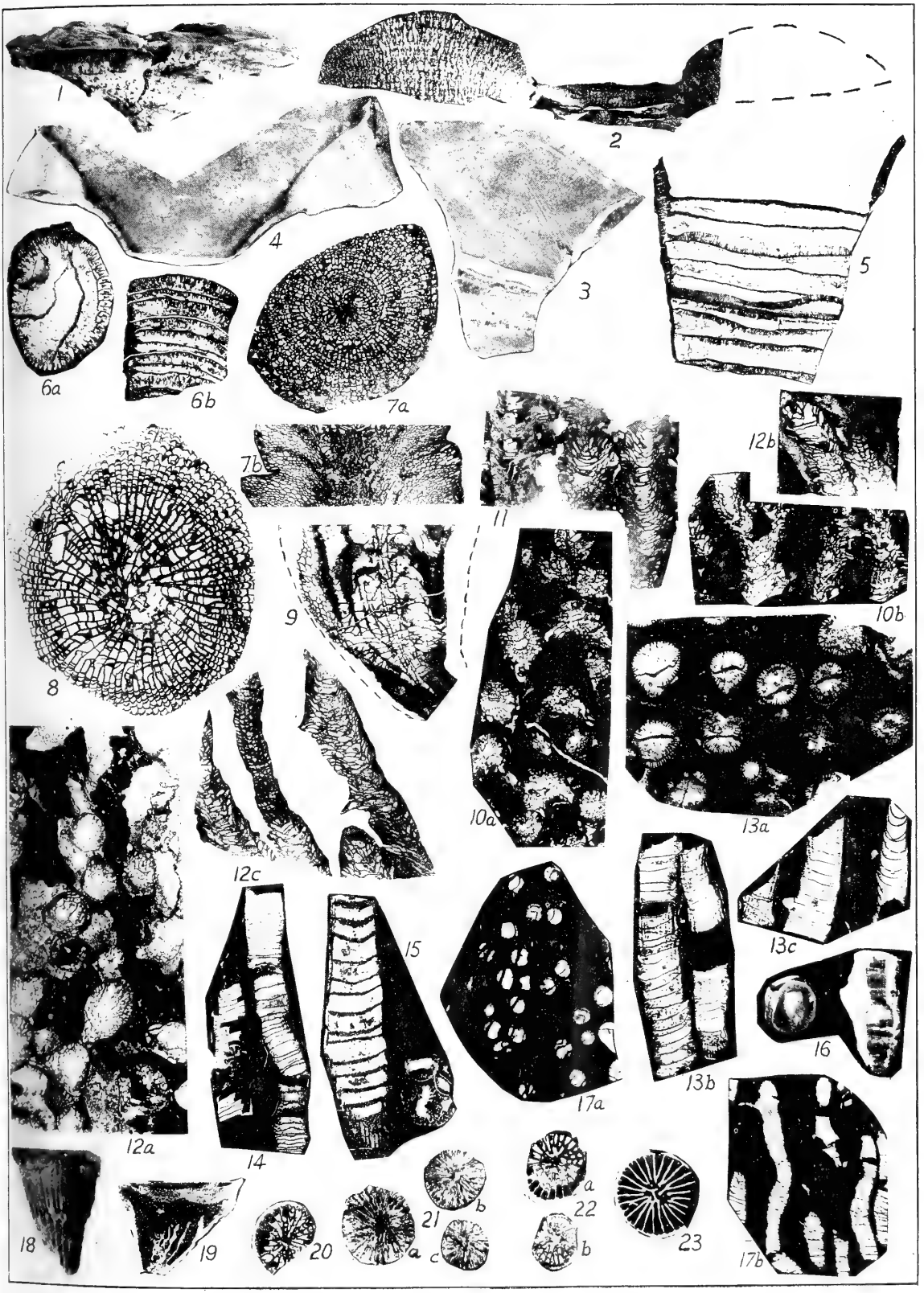
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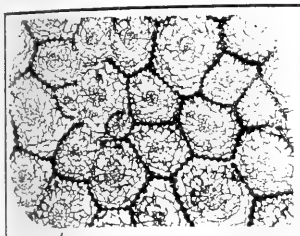
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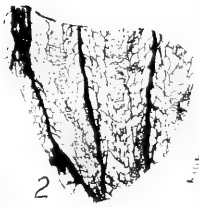
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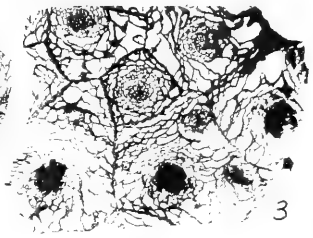
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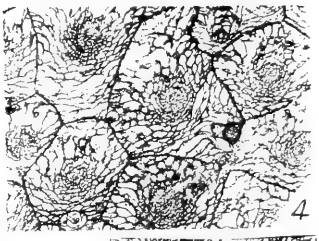
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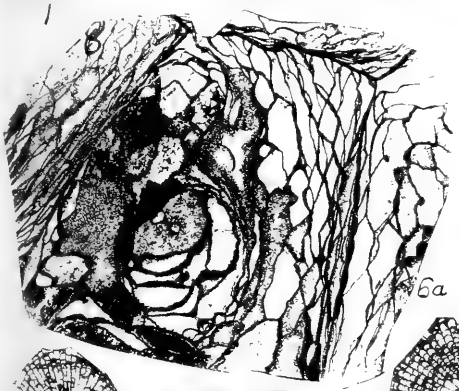
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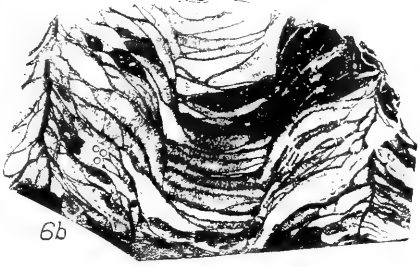
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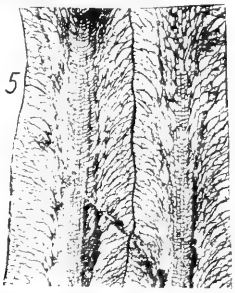
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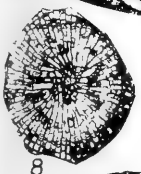
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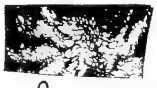
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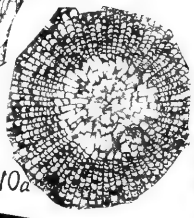
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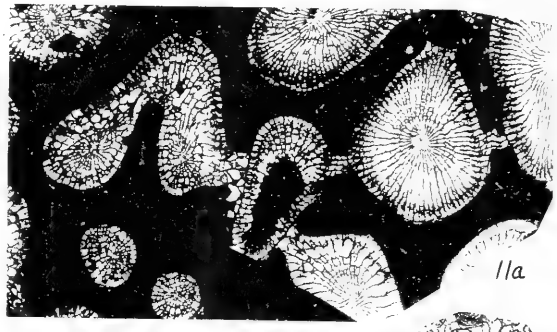
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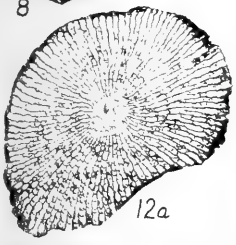
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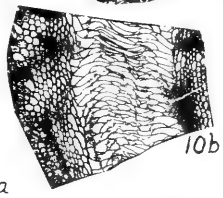
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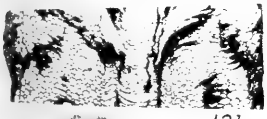
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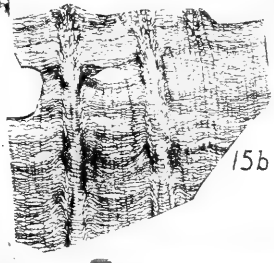
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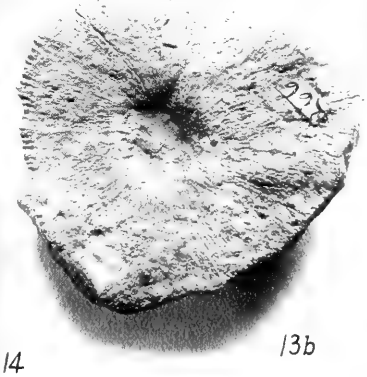
11b


16a

13a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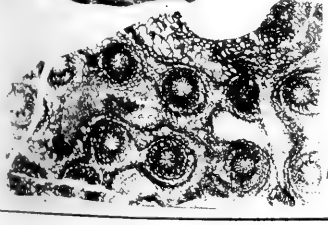
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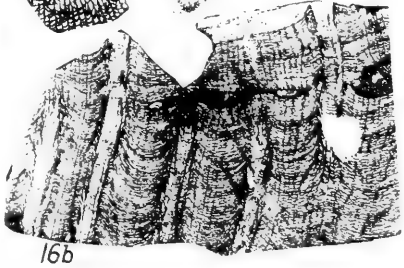

16b

REVISION OF AUSTRALIAN LEPIDOPTERA. OECOPHORIDAE. IX.

By A. Jefferis Turner, M.D., F.R.E.S.

[Read 25th September, 1940.]

A few errors and omissions must be recorded.

697. Eulechria droserodes Low. should be transferred to *Coesyra*, where it should follow *C. paragypsa*.

698. The locality for *Eulechria amphisema* Low. is Townsville, not Broken Hill.

901. In naming this species *E. maesta* I overlooked the fact that I had already used this name for species 879. I therefore propose to rename it Eulechria egena (*egenus*, needy).

1022. Pachybela maculisarca Low., P.L.S.N.S.W., 1915, p. 481 (Broken Hill, Pinnaroo).

1023. Antiopala xanthospila Turn., ibid., 1916, p. 257 (Macpherson Range, Ebor).

1024. Antiopala furtiva, n. sp. (*furtivus*, concealed.)

♂. 12–14 mm. Head fuscous; face paler, sometimes whitish. Palpi with terminal joint nearly as long as second; whitish. Antennae fuscous; ciliations in male one and a half. Thorax fuscous. Abdomen grey; tuft whitish. Legs fuscous with whitish rings; posterior pair whitish. Forewings with costa gently arched, apex rounded, termen oblique; whitish, generally suffused with fuscous in most examples obscuring markings, but in some these are more distinct; some basal suffusion; first discal at one-fourth, plical beneath it, second discal about middle; postmedian and subterminal fasciae, broader on costa; cilia mixed with fuscous or wholly fuscous. Hindwings and cilia grey.

New South Wales: Ebor in December; seven specimens.

The present instalment contains three large genera, *Machaeretis*,* *Ocystola*, and *Coesyra*, together with a number of smaller genera related to them.

Key to the Genera (continuing that given in Part viii).

17.	Palpi with second joint rough-scaled anteriorly	18
	Palpi with second joint not rough-scaled anteriorly	22
18.	Palpi very short, terminal joint not reaching vertex	*Psaltriodes*
	Palpi with terminal joint exceeding vertex	19
19.	Hindwings elongate-ovate or broadly ovate	*Pachybela*
	Hindwings lanceolate	20
20.	Hindwings with 3 and 4 separate	*Acorotricha*
	Hindwings with 3 and 4 not separate	21
21.	Palpi rough beyond middle anteriorly, hindwings with 3 and 4 stalked	*Acedesta*
	Palpi rough at apex only, hindwings with 3 and 4 connate	*Oxythecta*
22.	Hindwings lanceolate	23
	Hindwings elongate-ovate	36
23.	Antennae without basal pecten	*Eulachna*
	Antennae with basal pecten	24
24.	Hindwings with 5 absent	*Eccoena*
	Hindwings with 5 present	25
25.	Hindwings with 4 absent	*Microlocha*
	Hindwings with 4 present	26
26.	Forewings with 4 absent	*Stenophara*
	Forewings with 4 present	27
27.	Antennae of male deeply notched near base	*Rhoecoceros*
	Antennae of male not notched	28
28.	Palpi with second joint not reaching base of antennae	29
	Palpi with second joint reaching base of antennae	33
29.	Palpi with terminal joint shorter than second	30
	Palpi with terminal joint as long as second	*Tachystola*

* This name has been incorrectly spelt throughout this paper, and I regret the error. It should be *Machaeritis*.—A.J.T.

30. Forewings with raised scales ..... *Heterozyga*
Forewings without raised scales 31
31. Hindwings with 3 and 4 separate ..... *Oxybeles*
Hindwings with 3 and 4 connate 32
32. Abdomen in male with large posterior tuft on dorsum ..... *Dasycerca*
Abdomen in male without dorsal tuft ..... *Machaeretis*
33. Palpi with terminal joint minute ..... *Spaniacma*
Palpi with terminal joint moderate or long 34
34. Hindwings with 3 and 4 separate ..... *Antiterpna*
Hindwings with 3 and 4 not separate 35
35. Palpi with second joint thickened throughout with appressed scales ..... *Opsitycha*
Palpi with second joint slender ..... *Ocystola*
36. Antennae without basal pecten 37
Antennae with basal pecten 39
37. Tongue absent ..... *Sphaerelictis*
Tongue present 38
38. Anterior tibiae thickened with scales ..... *Aristeis*
Anterior tibiae not thickened ..... *Antiopala*
39. Hindwings with 4 absent ..... *Periorycta*
Hindwings with 4 present 40
40. Forewings with 10 absent ..... *Syscalma*
Forewings with 10 present 41
41. Palpi with second joint not reaching base of antennae 42
Palpi reaching base of antennae 47
42. Palpi with terminal joint one-third or less 43
Palpi with terminal joint one-half or more 44
43. Palpi with terminal joint minute ..... *Hemibela*
Palpi with terminal joint not less than one-fourth ..... *Hippomacha*
44. Antennae with pecten large and dense, covering front of eye ..... *Calypta*
Antennae with pecten normal 45
45. Anterior tibiae and tarsi dilated with dense scales ..... *Crepidosceles*
Anterior tibiae and tarsi not dilated 46
46. Hindwings with 6 and 7 approximated at origin ..... *Olbonoma*
Hindwings with 6 and 7 not approximated ..... *Coesyra*

86. Gen. Acorotricha Meyr. (*Exot. Micro.*, i, p. 121.)

Palpi long, recurved, ascending; second joint reaching base of antennae, rough-scaled beneath towards apex; terminal joint shorter than second, slender, acute. Antennae four-fifths; in male with extremely long ciliations; basal joint with strong pecten. Forewings with 7 to termen. Hindwings lanceolate; 3 and 4 rather remote, 5, 6, 7 nearly parallel, 7 to apex. Monotypical.

1025.† Acorotricha crystanta Meyr., *Exot. Micro.*, i, p. 121 (Cairns).

87. Gen. Acedesta, n.g. (ἀκηδεστος, neglected.)

Palpi moderate, curved, ascending; second joint not reaching base of antennae, thickened and rough-scaled anteriorly from middle to apex; terminal joint less than one-half, slender, acute. Antennae with strong basal pecten. Forewings with 2 from well before angle, 7 to termen. Hindwings lanceolate, pointed; 3 and 4 stalked.

1026. Acedesta picicolor, n. sp. (*picicolor*, pitch-black.)

♂. 17 mm. Head and thorax dark fuscous. Palpi dark fuscous. Antennae fuscous; ciliations in male 2. (Abdomen missing.) Legs fuscous; posterior pair grey. Forewings narrow, costa gently arched, apex rounded, termen obliquely rounded; dark fuscous; cilia dark fuscous. Hindwings narrowly lanceolate; fuscous; cilia fuscous.

Queensland: Yeppoon in October; one specimen.

88. Gen. Oxythecta Meyr. (P.L.S.N.S.W., 1884, p. 1048.)

Palpi long, recurved, ascending; second joint not reaching base of antennae, expanded towards apex, which is rough-scaled beneath; terminal joint as long as second. Antennae with basal pecten. Forewings with 7 to termen; upper basal fork of 1 obsolete. Hindwings rather broadly lanceolate, pointed. Type, *O. acceptella* Wlk. Eight species.

1027. Oxythecta hieroglyphica Meyr., P.L.S.N.S.W., 1884, p. 1052 (Cairns to Victoria, Tasmania, and South and South-west Australia).

1028. Oxythecta lygrosema Meyr., ibid., 1884, p. 1054 (Brisbane to Melbourne).

1029. Oxythecta zonoteles Meyr., ibid., 1884, p. 1053 (Sydney, Katoomba, Jervis Bay).

1030. Oxythecta acceptella Wlk., xxix, p. 694; Meyr., ibid., 1884, p. 1054 = *connexella* Wlk., xxix, p. 695 = *abstersella* Wlk., xxix, p. 762 (Nambour to Melbourne).

1031. Oxythecta alternella Wlk., xxix, p. 682; Meyr., ibid., 1884, p. 1050 (Mt. Tamborine and Stanthorpe to Victoria and Tasmania).

1032. Oxythecta nephelonota Meyr., ibid., 1884, p. 1051 (Tasmania).

1033. Oxythecta loxomochla, n. sp. (λοξόμοχλος, obliquely barred.)

♂. 18 mm. Head white with a fuscous spot on crown and another on lower end of face. Palpi dark fuscous; apex of second and basal three-fourths of terminal joint white. Antennae fuscous annulated with whitish; ciliations in male 3. Thorax white sprinkled with dark fuscous. Abdomen pale grey; apices of segments and tuft whitish. Legs fuscous; posterior pair mostly whitish. Forewings narrow, slightly dilated, costa gently arched, apex acute, termen straight, strongly oblique; white with dark fuscous irroration and markings; a small basal fascia shortly produced on costa; an oblique fascia from one-third costa towards one-fourth dorsum ending on fold; three quadrangular costal spots beyond middle; a short erect bar from just before tornus; a longer oblique bar from near termen shortly above tornus to near first costal spot; a series of three or four subterminal dots; cilia grey, bases white with some dark fuscous points, apices white. Hindwings and cilia pale grey. Nearest *O. nephelota*, but readily distinguished by the tornal bars.

Victoria: Gisborne in March; one specimen. Type in Coll. Lyell.

1034. Oxythecta amblyteles Meyr., P.L.S.N.S.W., 1888, p. 1662 (Duaringa, Miles).

89. Gen. Psaltriodes Meyr. (*Tr.R.S.S.Aust.*, 1902, p. 137.)

Tongue short. Palpi with second joint reaching only to middle of face, with short rough projecting scales beneath; terminal joint not reaching vertex, slender, acute. Antennae with basal pecten. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Monotypical. The exact position of this genus, which I have not been able to examine, is doubtful.

1035.† Psaltriodes thriambis Meyr., *Tr.R.S.S.Aust.*, 1902, p. 138 (Duaringa).

90. Gen. Eulachna Meyr. (*Ibid.*, 1884, p. 761.)

Palpi moderate, curved, ascending, smooth, slender; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae without basal pecten. Forewings with 7 to termen. Hindwings lanceolate, pointed; cilia over 1. Type, *E. dasyptera*.

1036. Eulachna dasyptera Meyr., ibid., 1884, p. 761 (Duaringa, Brisbane, Sydney, Wollongong, Katoomba).

1037. Eulachna droseropa, n. sp. (δροσερωπος, bedewed.)

♂. 11–12 mm. Head pale ochreous. Palpi with terminal joint one-half; ochreous-fuscous. Antennae fuscous; ciliations in male 2. Thorax and abdomen fuscous. Legs grey; posterior pair ochreous-whitish. Forewings suboval, costa moderately arched, apex pointed, termen oblique; whitish-ochreous finely sprinkled with grey; cilia concolorous. Hindwings lanceolate; dark grey; cilia 1, grey with a darker basal line.

Queensland: Yeppoon in September; two specimens.

91. Gen. Eccoena, n.g. (ἐκκοινος, out of the ordinary.)

Tongue present. Palpi rather short, curved, slender; second joint not reaching base of antennae; terminal joint less than one-half, acute. (Antennae probably with basal pecten, but if so, this has been denuded in the type specimen.) Forewings narrow, triangularly dilated, apex acute and produced, termen incurved, oblique; 7 to termen. Hindwings narrowly lanceolate; 3 and 4 connate, 5 absent, 6 and 7 well separate at origin, at first parallel, then diverging, 6 being parallel to 4. This genus is not at all closely related to *Microlocha*, and in this instance it is clearly 5 that is missing and not 4.

1038. Eccoena trigonoptera, n. sp. (*τριγωνοπτερος*, with triangular wings.)

♀. 17 mm. Head and thorax fuscous. Palpi whitish. Antennae grey. (Abdomen missing.) Legs whitish; anterior pair grey. Forewings narrowly triangular; fuscous; a narrow white costal streak from near base to three-fourths; a suboval orange spot on tornus reaching two-thirds across to costa, its upper anterior angle joined by a fine longitudinal orange line from mid-disc; cilia yellow, bases orange, on apex and tornus fuscous. Hindwings and cilia dark grey.

Queensland: Toowoomba in November; one specimen received from Mr. W. B. Barnard.

92. Gen. Microlocha Meyr. (*Exot. Micro.*, i, p. 241.)

Palpi moderate, curved, ascending; second joint not reaching base of antennae, thickened with appressed scales; terminal joint shorter than second, moderately stout, acute. Antennae with strong pecten. Forewings with 7 to termen. Hindwings lanceolate, pointed; 4 absent; cilia 2. Monotypical.

1039.† Microlocha entypa Meyr., *Exot. Micro.*, i, p. 241 (Darwin).

93. Gen. Stenophara, n.g. (*στενοφαρος*, in slender cloak.)

Palpi moderate, curved, ascending, smooth, slender; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae with basal pecten. Forewings with 4 absent, 7 to termen. Hindwings lanceolate; 3 and 4 stalked.

1040. Stenophara euneta, n. sp. (*εὐνητος*, well spun.)

♂. 12–14 mm. Head blackish; face white. Palpi white, apex of terminal joint blackish. Antennae blackish; ciliations in male one and a quarter. Thorax white, anterior edge blackish. Abdomen grey. Legs fuscous with whitish rings; posterior pair whitish. Forewings narrow, costa gently arched, apex rounded, termen very obliquely rounded, white with blackish markings; base of costa blackish; a transverse fascia at one-third, expanded on dorsum; a narrower fascia from four-fifths costa to tornus; a small apical blotch not reaching tornus, variably mixed with white on termen; cilia ochreous-whitish. Hindwings and cilia pale grey. In one example 4 and 5 are stalked in one forewing only.

Queensland: Bunya Mts. (3000 ft.) in January; Macpherson Range (3500 ft.) in December and January; eight specimens.

94. Gen. Rhoecoceros, n.g. (*ῥοικεκερως*, with crooked horns.)

Palpi rather short, curved, ascending, smooth, slender; second joint not nearly reaching base of antennae, terminal joint one-half. Antennae in male with a deep U-shaped notch on dorsum near base, curved at notch, ciliations long; with basal pecten. Forewings with 7 to termen. Hindwings lanceolate.

1041. Rhoecoceros pelomorpha, n. sp. (*πηλομορφος*, clay-coloured.)

♂. 14 mm. Head, palpi, and thorax brown. Antennae grey; ciliations in male 4. Abdomen and legs brown. Forewings narrow, costa slightly arched, apex obtusely pointed, termen oblique; brown; discals fuscous, minute, first at one-third, plical before it, second at middle; a fuscous dot on three-fourths dorsum; a suffused fuscous spot on four-fifths costa; cilia brown with a fuscous median line. Hindwings and cilia grey.

Queensland: Caloundra in September; one specimen.

95. Gen. Heterozyga Meyr. (P.L.S.N.S.W., 1884, p. 1047.)

Palpi moderate, recurved, ascending, slender; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae with basal pecten. Forewings with small tufts of scales; 7 to termen. Hindwings rather broadly lanceolate, pointed. Type, *P. coppatias*. Meyrick records six species from India and Ceylon and one from South Africa.

1042.† Heterozyga arida Meyr., *Tr.R.S.S.Aust.*, 1902, p. 137 (W.A.: Carnarvon).

1043. Heterozyga coppatias Meyr., P.L.S.N.S.W., 1884, p. 1049 (Bathurst, Adelaide, Mt. Lofty; W.A.: York).

96. Gen. Dasycerca Turn. (P.L.S.N.S.W., 1914, p. 555.)

Palpi rather short, curved, ascending, smooth, slender; second joint not nearly reaching base of antennae; terminal joint shorter than second, acute. Antennae with

basal pecten. Forewings with 7 to termen. Hindwings rather broadly lanceolate, pointed. Abdomen in male with a large dense posterior tuft of scales on dorsum. Monotypical.

1044. DASYCERCA APOCRYPHA Turn., ibid., 1914, p. 555 (Mt. Tamborine, Ebor).

97. Gen. MACHAERETIS Meyr. (P.L.S.N.S.W., 1885, p. 766.)

Palpi moderate, curved, ascending, smooth, slender; second joint not reaching base of antennae; terminal joint shorter than second. Antennae with basal pecten; ciliations in male long, moderate, or short. Forewings with 7 to termen. Hindwings lanceolate; cilia one to one and a half. Type *M. aegrella* Meyr. This is a difficult genus, and much care is necessary in discriminating its species. It is a direct derivative of *Coesyra* and exclusively Australian. Seventy-two species.

1045. MACHAERETIS OXYTORA Meyr., ibid., 1884, p. 1064 (Nambour to Gisborne).

1046. MACHAERETIS COSMOZONA, n. sp. (*κοσμοζωνος*, neatly girdled.)

♂, ♀. 10–12 mm. Head pale yellow. Palpi with terminal joint one-half; pale yellow. Antennae grey; ciliations in male 3. Thorax pale yellow, anterior edge fuscous. Abdomen fuscous; tuft whitish. Legs whitish-ochreous; anterior pair fuscous. Forewings narrow, posteriorly dilated costa straight to near apex, apex acute, termen straight, strongly oblique; pale yellow; costal edge blackish towards base; two narrow brownish transverse fasciae; first from two-fifths costa to mid-dorsum; second from four-fifths costa to tornus; median area lightly suffused with brownish-fuscous; termen narrowly brownish-fuscous; cilia brownish. Hindwings and cilia grey.

Queensland: Brisbane in November; Toowoomba in October, November and February; six specimens.

1047. MACHAERETIS HEMISEMA Meyr., ibid., 1884, p. 1061 (Herberton; Brisbane to Tasmania, South Australia and Western Australia).

1048.† MACHAERETIS MILICHIA Meyr., ibid., 1884, p. 1071 (Katoomba).

1049. MACHAERETIS PSAMATHINA Meyr., ibid., 1884, p. 1070 (Atherton Plateau to Melbourne and Mt. Lofty).

1050.† MACHAERETIS AGELAEA Meyr., ibid., 1884, p. 1070 (Deloraine, Tas.).

1051. MACHAERETIS XERODES Low., ibid., 1900, p. 414 (Birchip, Broken Hill).

1052.† MACHAERETIS NEPHELORA Meyr., ibid., 1888, p. 1668 (York, W.A.).

1053.† MACHAERETIS HOMALOPIS Meyr., ibid., 1888, p. 1668 (York, W.A.).

1054. MACHAERETIS PELINOPA Meyr., *Tr.R.S.S.Aust.*, 1902, p. 133 (Tasmania).

1055. MACHAERETIS HOMOLEUCA Meyr., P.L.S.N.S.W., 1884, p. 1076 (Glen Innes to Victoria, South Australia, and Western Australia).

1056. MACHAERETIS INDOCTA Meyr., ibid., 1885, p. 772 (Brisbane, Tweed Hds., Toowoomba, Killarney, Bunya Mts.).

1057.† MACHAERETIS SYNORA Meyr., ibid., 1888, p. 1668 (W.A.: Perth).

1058. MACHAERETIS AEGRELLA Meyr., ibid., 1885, p. 772 (Toowoomba to Victoria, Tasmania and South and Western Australia).

1059. MACHAERETIS HAPLOPA, n. sp. (*ἁπλωπος*, simple.)

♂. 12–13 mm. Head fuscous; face whitish. Palpi fuscous; terminal joint whitish anteriorly. Antennae grey; ciliations in male less than one-half. Thorax fuscous. Abdomen grey. Legs fuscous; posterior pair ochreous-whitish. Forewings narrow, apex obtusely pointed; whitish sprinkled with grey; stigmata fuscous, discals approximated, first at middle, second at two-thirds, plical well before first discal, but sometimes obsolete; cilia concolorous. Hindwings and cilia pale grey. Forewings whiter than in *M. aegrella* and without ochreous tinge. Best distinguished by the very short antennal ciliations (in *aegrella* 1).

Queensland: Chinchilla in October; five specimens.

1060. MACHAERETIS PARASTATIS, n. sp. (*παραστατις*, an ally.)

♂. 12–14 mm. Head and thorax grey-whitish. Palpi with terminal joint three-fifths; grey-whitish. Antennae grey; ciliations in male 2. Abdomen grey. Legs grey; posterior pair whitish. Forewings narrow, apex obtuse; whitish sprinkled with grey; stigmata fuscous, first discal represented by a short longitudinal streak at two-fifths,

plical beneath it, but both may be obsolete, second discal at two-thirds; cilia concolorous. Hindwings and cilia pale grey. Very similar to the preceding, but the longer antennal ciliations furnish a good distinction.

Queensland: Caloundra in September; Tweed Hds. and Toowoomba in August; Mitchell in September. New South Wales: Sydney in August. Five specimens.

1061.† MACHAERETIS CONIATA Meyr., ibid., 1884, p. 1069 (Deloraine, Mt. Wellington).

1062.† MACHAERETIS DYSTECHNA Meyr., ibid., 1888, p. 1664 (Sydney, Katoomba).

1063.† MACHAERETIS HEMERA Meyr., ibid., 1885, p. 771 (Pt. Lincoln).

1064. MACHAERETIS COMPSA Turn., *P.R.S.Tas.*, 1938, p. 92 (Russell Falls, Lake Fenton 4000 ft., Cradle Mt. 3000 ft.).

1065. MACHAERETIS PSATHYRA Meyr., 1885, p. 771 (Hobart; W.A.: Albany).

1066.† MACHAERETIS DOXASTICA Meyr., ibid., 1888, p. 1667 (W.A.: Albany).

1067. MACHAERETIS XANTHOPASTA, n. sp. (*ξανθοπαστος*, sprinkled with yellow.)

♀. 11 mm. Head ochreous-yellow. Palpi with second joint not nearly reaching base of antennae, terminal joint three-fifths; fuscous. Antennae and thorax fuscous. (Abdomen missing). Legs fuscous with whitish-ochreous rings. Forewings suboblong, costa arched near base, thence straight, apex rounded, termen obliquely rounded; whitish-grey densely sprinkled with dark fuscous and yellowish scales; these form three transverse fasciae, at two-fifths, three-fifths, and before apex; cilia grey. Hindwings lanceolate; dark grey; cilia dark grey.

Queensland: Yeppoon in September; one specimen.

1068. MACHAERETIS ENCRITA Low., *T.R.S.S.Aust.*, 1920, p. 65 (Birchip; Broken Hill).

1069. MACHAERETIS NIPHODESMA Meyr., ibid., 1884, p. 1080 (Duaringa; Sydney).

1070.† MACHAERETIS DICLETHRA Meyr., ibid., 1884, p. 1079 (Sydney).

1071. MACHAERETIS GAMELIA, n. sp. (*γαμηλιος*, in bridal array.)

♂. 12–13 mm. Head and thorax white. Palpi pale fuscous; terminal joint one-half. white. Antennae white; ciliations in male less than one-half. Abdomen whitish. Legs pale fuscous; posterior pair whitish. Forewings narrow, apex obtuse; white without irroration; a short inwardly oblique streak from costa before apex, a tornal spot, and some terminal dots pale ochreous-fuscous; cilia white. Hindwings and cilia whitish-grey. Best distinguished from *M. indocta*, in which the antennal ciliations are equally short, by the absence of antennal annulations; also by the clear whiteness of the forewings.

New South Wales: Tabulam in December; Canberra in February; two specimens.

1072. MACHAERETIS HYPERLEUCA, n. sp. (*ὑπερλευκος*, very white.)

♂. 13 mm. Head and palpi white. Palpi with terminal joint three-fourths; white, external surface of second joint except apex fuscous. Antennae pale grey; ciliations in male less than one-half. Abdomen white; bases of segments and tuft grey. Legs fuscous; posterior pair whitish. Forewings with costa moderately arched, apex pointed, termen very oblique; white; a minute supramedian fuscous dot; cilia white. Hindwings and cilia whitish.

Queensland: Rockhampton in August; one specimen.

1073. MACHAERETIS LINIGERA, n. sp. (*linigerus*, clothed in linen.)

♂. 13 mm. Head and thorax white. Palpi with terminal joint three-fourths; white, second joint except apex fuscous. Antennae whitish; ciliations in male 3. Abdomen grey; apices of segments and tuft white. Legs fuscous (posterior pair missing). Forewings narrow, costa slightly arched, apex acute, termen very oblique; white; cilia white. Hindwings and cilia white. Differs from both the preceding species in its long antennal ciliations.

Queensland: Dalby in October; one specimen.

1074. MACHAERETIS COSTIPUNCTA, n. sp. (*costipunctus*, with costal dot.)

♂. 11 mm. Head and thorax white. Palpi with terminal joint two-thirds; white. Antennae grey; ciliations in male 1. Abdomen grey. Legs whitish; anterior pair fuscous. Forewings with costa slightly arched, apex round-pointed, termen obliquely rounded; white very sparsely sprinkled with fuscous, more so on costal edge; a fuscous

dot on costa at three-fourths; terminal edge and cilia faintly ochreous-tinged. Hindwings and cilia white.

North Queensland: Eungella in October; one specimen.

1074*a*. MACHAERETIS NAIAS Meyr., *Tr.R.S.S.Aust.*, 1902, p. 134 (Macpherson Range, Mt. Kosciusko 5000 ft., Gisborne).

1075. MACHAERETIS PISSOGRAMMA, n. sp. (*πισσογραμμος*, with pitch-black markings.)

♀. 12 mm. Head white. Palpi with second joint slightly thickened, terminal joint three-fifths; white, base and two dots on outer side of second joint beyond middle, basal and subapical rings and apex of terminal joint fuscous. Antennae blackish. Thorax white with a few blackish scales anteriorly. Abdomen grey; tuft whitish. Legs fuscous with white rings; posterior pair mostly white. Forewings narrow, costa almost straight, apex rounded, termen very obliquely rounded; white with blackish markings and irroration; a sub-basal fascia connected with bases of costa and dorsum; costal dots at one-fourth and middle giving rise to very suffused oblique fasciae; an oblique line from costa before apex joining third fascia on dorsum; a discal dot between third and fourth fasciae; a larger dot beyond and touching fourth fascia; three terminal dots more or less connected; cilia white with a few blackish points. Hindwings narrowly lanceolate; pale grey; cilia pale grey.

Queensland: Toowoomba in October; one specimen received from Mr. W. B. Barnard.

1076. MACHAERETIS ASSULOSA, n. sp. (*assulosus*, like a splinter.)

♂. 12 mm. Head and thorax white. Palpi with terminal joint one-half; whitish. Antennae pale grey; ciliations in male 3. Abdomen pale grey; tuft whitish. Legs whitish; anterior pair fuscous. Forewings very narrow, apex pointed, termen oblique; white with fine sparse blackish irroration; stigmata fuscous, indistinct, first discal at one-third, plical beyond it, second discal at two-thirds; cilia white with fuscous points. Hindwings narrowly lanceolate; whitish-grey; cilia one and a half, whitish-grey. Both wings are narrower than in *M. melanospora*, the forewings irrorated with blackish scales without ochreous tinge, and the antennal ciliations are much longer.

Queensland: Sandgate near Brisbane in September; one specimen.

1077. MACHAERETIS MELANOSPORA Meyr., ibid., 1885, p. 770 (Yeppoon to Sydney).

1078. MACHAERETIS SAMPHORAS Meyr., ibid., 1885, p. 770 (Palm Is. to Tasmania).

1079. MACHAERETIS ARGOPTERA, n. sp. (*ἀργοπτερος*, white-winged.)

♂. 15 mm. Head and thorax white. Palpi with terminal joint one-half; white, basal half of second joint and a median ring on terminal joint fuscous. Antennae grey; ciliations in male one-half. Abdomen grey-whitish. Legs fuscous; tibiae and tarsi with whitish rings; posterior pair mostly whitish. Forewings narrow, elongate, costa scarcely arched, apex acute, termen very oblique; white with dark fuscous markings; a costal streak interrupted at one-fourth and two-thirds and not reaching apex; a dot on base of dorsum; first discal at one-third, second before two-thirds, plical absent; cilia white, on tornus grey. Hindwings and cilia whitish. The palpi have second joint somewhat expanded towards apex but smooth-scaled.

Queensland: Macpherson Range in November; one specimen received from Mr. W. B. Barnard.

1080. MACHAERETIS NIPHOESSA, n. sp. (*νιφοεις*, snow-white.)

♂. 12–13 mm. Head and thorax white. Palpi with terminal joint one-half; white, outer surface of second joint except base and apex fuscous. Antennae grey; ciliations in male 3. Abdomen grey; tuft white. Legs whitish; anterior pair fuscous. Forewings very narrow, costa nearly straight, apex pointed, termen oblique; snow-white; two moderate ochreous-fuscous fasciae; first from one-third dorsum towards but not reaching costa before middle; second from two-thirds costa dividing above tornus, its branches reaching dorsum and termen respectively; cilia pale ochreous-fuscous, on tornus white. Hindwings and cilia grey-whitish.

Queensland: Toowoomba in October; Stanthorpe in November; two specimens received from Mr. W. B. Barnard.

1081. MACHAERETIS INGRATA Meyr., *Exot. Micro.*, i, p. 117 (Gisborne).

1082. MACHAERETIS MICROPTILA, n. sp. (*μικροπτιλος*, small-winged.)

♀. 11 mm. Head and thorax ochreous-grey-whitish. Palpi whitish; basal half and a subapical ring on second joint and a sub-basal ring and apex of terminal joint blackish. Abdomen grey. Legs fuscous; tarsi with whitish rings; posterior pair mostly whitish. Forewings narrow-elongate-oval, costa moderately arched, apex pointed, termen very obliquely rounded; ochreous-grey-whitish with some fuscous irroration; short fuscous marks on costa at one-fourth, middle, and three-fourths; first discal at one-third, plical before it, second discal at two-thirds; cilia grey-whitish with a few fuscous points. Hindwings and cilia grey. Very small and obscure; best recognized by the marks on costa.

Queensland: Macpherson Range (3500 ft.) in December; one specimen.

1083. MACHAERETIS ACIBDELA, n. sp. (*ἀκιβδηλος*, unmarked.)

♂, ♀. 14 mm. Head and thorax white. Palpi fuscous; terminal joint two-thirds, white. Antennae grey; ciliations in male extremely minute. Abdomen grey. Legs fuscous; posterior pair whitish. Forewings moderate, apex obtuse; white without ochreous tinge finely sprinkled with grey; cilia white. Hindwings broadly lanceolate, apex pointed; pale grey; cilia pale grey. The extremely minute antennal ciliations are a very unusual character in this group.

Queensland: Quilpie in August; three specimens.

1084.† MACHAERETIS APOTHYMA Meyr., ibid., 1884, p. 787 (S.A.: Petersburg).

1085.† MACHAERETIS HEPTACHORA Meyr., *Exot. Micro.*, i, p. 301 (Pt. Lincoln).

1086. MACHAERETIS PROSECHES, n. sp. (*προσεχης*, adjoining.)

♂. 14 mm. Head and thorax whitish. Palpi with terminal joint one-half; whitish. Antennae whitish with fuscous annulations; ciliations in male 1. Abdomen grey-whitish. Legs whitish; anterior pair fuscous. Forewings narrow, apex pointed; white with minute stigmata and scanty irroration fuscous; first discal at one-third, plical beneath it, second discal at two-thirds; cilia white with a few fuscous points. Hindwings and cilia whitish.

New South Wales: Mt. Wilson in November; three specimens.

1087. MACHAERETIS CALLICYPHA, n. sp. (*καλλικυφος*, beautifully arched.)

♂. 21 mm. Head and thorax ochreous-whitish. Palpi pale fuscous; terminal joint one-third, whitish. Antennae ochreous-whitish; ciliations in male 1. Abdomen pale grey, towards apex whitish. Legs ochreous-whitish; anterior pair pale fuscous. Forewings rather narrow, costa strongly arched, apex pointed, termen oblique; stigmata and scanty irroration fuscous; first discal at one-third, plical before it, both minute, second discal at two-thirds; cilia ochreous-whitish. Hindwings and cilia whitish.

North Queensland: Townsville in September; one specimen.

1088. MACHAERETIS HOMOMORPHA, n. sp. (*ὁμομορφος*, similarly formed.)

♂. 13 mm. Head and thorax white. Palpi with terminal joint two-thirds; whitish, outer surface of second joint except apex fuscous. Antennae whitish annulated with fuscous; ciliations in male two-thirds. Abdomen pale grey; tuft grey-whitish. Legs fuscous; posterior pair whitish. Forewings narrow, apex round-pointed; white; stigmata and scanty irroration fuscous; first discal at one-third, plical beyond it, second discal at two-thirds, a dot above and between discals; a small patch of irroration on two-thirds costa, some more before apex, termen, and tornus, with an indication of a subterminal line; cilia white. Hindwings and cilia grey-whitish.

Queensland: Killarney in November; one specimen.

1089. MACHAERETIS QUINQUEPUNCTIS, n. sp. (*quinquepunctis*, with five dots.)

♀. 11 mm. Head and thorax whitish. Palpi with terminal joint one-half; grey-whitish. Antennae whitish with fine fuscous annulations. Abdomen grey; tuft whitish. Legs grey; posterior pair whitish. Forewings narrow, apex round-pointed; white; stigmata and scanty irroration towards margins fuscous; first discal at one-third, plical beyond it; second discal at two-thirds, a dot above and midway between discals, and a fifth dot at five-sixths; cilia white. Hindwings whitish-grey; cilia whitish.

Queensland: Macpherson Range 3500 ft. in December; one specimen.

1090. MACHAERETIS HYLOBITA Turn., *Tr.R.S.S.Aust.*, 1917, p. 60 (Bunya Mts., Mt. Tamborine, Macpherson Range 3000 ft.).

1091. Machaeretis melanossa, n. sp. (*μελανοσσος*, black-eyed.)

♂. 12 mm. Head and thorax white. Palpi with terminal joint three-fourths; whitish. Antennae fuscous; ciliations in male 1. Abdomen whitish-grey. Legs fuscous; posterior pair whitish. Forewings moderate, apex pointed; white faintly ochreous-tinged; stigmata blackish, first discal at one-fourth, plical before it, second discal about middle; cilia white. Hindwings lanceolate; whitish; cilia 1, whitish.

Queensland: Toowoomba in October; one specimen.

1092. Machaeretis melanosparta, n. sp. (*μελανοσπαρτος*, sprinkled with black.)

♀. 10 mm. Head and thorax ochreous-whitish. Palpi with terminal joint one-half; ochreous-whitish. Antennae ochreous-whitish annulated with fuscous. Abdomen grey. Legs grey; posterior pair whitish. Forewings narrow, apex rounded; ochreous-whitish; stigmata and some sparsely scattered scales blackish; first discal at two-fifths, plical before it, second discal at two-thirds; several minute dots near tornus and apex; cilia ochreous-whitish with blackish points. Hindwings lanceolate; grey-whitish; cilia one and a half, grey-whitish.

Victoria: Beaconsfield in October; one specimen.

1093. Machaeretis orthosema, n. sp. (*ὀρθοσημος*, with a straight mark.)

♂. 10 mm. Head and thorax whitish-ochreous. Palpi with terminal joint three-fourths; ochreous-whitish. Antennae pale grey; ciliations in male one-half. Abdomen and legs ochreous-whitish. Forewings narrow, apex obtuse; stigmata and scanty irroration fuscous; first discal at two-fifths, plical before it, second discal at two-thirds, connected by a straight line with tornus; cilia concolorous. Hindwings narrowly lanceolate; grey-whitish; cilia grey-whitish.

North Queensland: Yungaburra (Atherton Plateau) in August; one specimen.

1094. Machaeretis heniocha Meyr., P.L.S.N.S.W., 1885, p. 769 (Cairns to Sydney).

1095. Machaeretis leptocneca, n. sp. (*λεπτοκνηκος*, faintly ochreous.)

♂. 12 mm. Head and thorax whitish-ochreous. Palpi with terminal joint one-half; whitish-ochreous. Antennae grey; ciliations in male one-half. Abdomen pale grey. Legs pale fuscous; posterior pair ochreous-whitish. Forewings moderate, apex obtuse; whitish-ochreous; stigmata and sparse irroration fuscous; first discal at one-third, plical beneath it, both minute, second discal well before two-thirds; some suffusion at base of costa; a suffused subterminal line from apex to tornus; cilia concolorous. Hindwings rather broadly lanceolate; whitish; cilia 1, whitish.

North Queensland: Herberton in June; one specimen.

1096. Machaeretis hypolepta, n. sp. (*ὑπολεπτος*, fine, delicate.)

♂. 7–8 mm. Head and thorax whitish. Palpi with terminal joint three-fifths; fuscous, apex of second and base and apex of terminal joint whitish. Antennae whitish annulated with fuscous; ciliations in male 1. Abdomen grey. Legs whitish; anterior pair with fuscous rings. Forewings posteriorly dilated, costa moderately arched, apex obtuse, termen obliquely rounded; whitish; markings and some irroration fuscous; a suffused spot on base of costa; an interrupted line from one-third costa to mid-dorsum; another from two-thirds costa to tornus; subapical and tornal spots, sometimes connected; cilia whitish with some fuscous scales. Hindwings lanceolate; grey; cilia over 1, grey.

North Queensland: Kuranda in October; Stannary Hills (Atherton Plateau); two specimens.

1097. Machaeretis platycapna, n. sp. (*πλατυκαπνος*, broadly fuscous.)

♂. 11 mm. Head dark fuscous on crown; face white. Palpi with terminal joint one-half; whitish, outer surface of second joint except apex fuscous. Antennae dark fuscous; ciliations in male 3. Thorax and abdomen dark fuscous. Legs fuscous. Forewings moderate, apex obtuse; dark fuscous; a broad sub-basal white fascia, narrower on dorsum; a rather large irregular-edged median white spot; cilia fuscous. Hindwings broadly lanceolate; fuscous-brown; cilia fuscous-brown.

Queensland: Chinchilla in October; one specimen.

1098. Machaeretis platyptila, n. sp. (*πλατυπτιλος*, broad-winged.)

♂. 11–13 mm. Head grey. Palpi with terminal joint three-fifths; fuscous. Antennae grey; ciliations in male 5. Thorax fuscous. Abdomen grey. Legs fuscous; posterior

pair ochreous-whitish. Forewings broadly oval, costa strongly arched, apex rounded, termen obliquely rounded; ochreous-whitish with fuscous markings; stigmata distinct, first discal at one-third, plical beneath it, second discal before two-thirds; a short oblique streak from tornus; a dot on five-sixths costa, from which a curved line sometimes proceeds to tornus; cilia ochreous-whitish with fuscous points. Hindwings and cilia grey.

New South Wales: Brunswick Hds. in December; three specimens received from Mr. W. B. Barnard, who has the type.

1099. MACHAERETIS TRISSOSPILA, n. sp. (*τρισσοσπιλος*, three-spotted.)

♂. 14 mm. Head white. Palpi with terminal joint one-fourth; whitish, second joint except base and apex fuscous. Antennae grey; ciliations in male 3. Thorax white; anterior edge fuscous. Abdomen grey. Legs whitish; anterior pair and tarsi fuscous with whitish rings. Forewings narrow, costa gently arched, apex pointed, termen straight, very oblique; white; markings and some irroration fuscous; a basal dorsal spot, another on dorsum at two-fifths, and a larger above tornus; some irroration along costa and termen; cilia white, apices and an antemedian line fuscous. Hindwings and cilia whitish-grey. The terminal joint of palpi is unusually short.

Queensland: Toowoomba in November; one specimen received from Mr. W. B. Barnard.

1100. MACHAERETIS PAVIDA, n. sp. (*pavidus*, timid.)

♂, ♀. 10–12 mm. Head pale yellowish. Palpi with terminal joint two-thirds; pale yellowish. Antennae pale yellowish with fuscous annulations; ciliations in male 3. Thorax fuscous. Abdomen grey. Legs pale ochreous; anterior pair fuscous. Forewings with costa strongly arched, apex round-pointed, termen obliquely rounded; pale yellowish with fuscous markings; a costal streak from base to one-third; a slender suffused median fascia, interrupted in middle; a tornal dot; a suffused subapical costal spot; some irroration before termen; cilia pale yellowish. Hindwings and cilia pale grey.

North Queensland: Malanda (Atherton Plateau) in August. Queensland: Macpherson Range (3500 ft.) in March. Five specimens.

1101. MACHAERETIS GRAMMOPHORA Meyr., P.L.S.N.S.W., 1885, p. 769 (Nambour to Lorne).

1102. MACHAERETIS DULCICULA Turn., *Tr.R.S.S.Aust.*, 1917, p. 60 (Macpherson Range, Ebor, Mt. Wilson, Melbourne).

1103. MACHAERETIS XANTHOMITRA, n. sp. (*ξανθομιτρος*, girdled with yellow.)

♂. 10 mm. Head orange. Palpi with terminal joint three-fifths; yellow, terminal joint fuscous. Antennae fuscous; ciliations in male 5. Thorax and abdomen fuscous. Legs fuscous with ochreous rings. Forewings slightly dilated, costa moderately arched, apex pointed, termen straight, oblique; fuscous with purple reflections and orange markings; a triangular sub-basal fascia from one-third costa becoming broader as it approaches dorsum; a dot on tornus and another above it; a fine line from costa before apex to midtermen, not reaching tornus; cilia fuscous. Hindwings and cilia fuscous.

New South Wales: Sydney in October; two specimens received from Mr. G. M. Goldfinch, who has the type.

1104. MACHAERETIS PERCARA, n. sp. (*percarus*, very dear.)

♂. 12 mm. Head pale yellow. Palpi with terminal joint three-fifths; ochreous-whitish, second joint except apex fuscous. Antennae fuscous; ciliations in male one-half. Thorax and abdomen dark fuscous. Legs fuscous; posterior pair mostly ochreous-whitish. Forewings slightly dilated, costa gently arched, apex rounded, termen obliquely rounded; pale yellow with fuscous markings; a basal fascia prolonged on costa to one-third; a broad fascia from costa beyond middle to tornus; a terminal fascia separated from second by a pale yellow line, confluent with it on tornus; cilia fuscous. Hindwings broadly lanceolate; grey; cilia grey.

Queensland: Rosewood in April; one specimen.

1105. MACHAERETIS CALLIGENES Meyr., ibid., 1885, p. 768 = *calliphylla* Turn., *Tr.R.S.S.Aust.*, 1917, p. 59 (Brisbane to Victoria, Launceston, and Pt. Lincoln).—This

species is variable. The thorax, which is usually fuscous anteriorly and yellow posteriorly, may be either wholly fuscous or wholly yellow; the forewings may have an additional sub-basal fascia.

1106. MACHAERETIS INSOLITA, n. sp. (*insolitus*, unusual.)

♂. 16 mm. Head white. Palpi with terminal joint three-fifths; whitish, second joint except apex fuscous. Antennae fuscous; ciliations in male 3. Thorax and abdomen fuscous. Legs fuscous; posterior pair whitish. Forewings narrow, posteriorly dilated, costa nearly straight, apex pointed, termen straight, oblique; white; markings fuscous; a costal streak from base to middle, where it forms a triangular spot; an oblique streak from mid-dorsum half across disc; a circular discal blotch at three-fourths, connected with four-fifths costa; a terminal line interrupted above tornus; cilia fuscous, apices except on tornus whitish. Hindwings and cilia grey.

Western Australia: Albany in February; one specimen received from Mr. W. B. Barnard.

1107. MACHAERETIS NEUROTA Meyr., P.L.S.N.S.W., 1884, p. 1082 = *albida* Turn., *Tr.R.S.S.Aust.*, 1896, p. 15 (Duaringa to Victoria).

1108. MACHAERETIS STENOPTERA Meyr., ibid., 1884, p. 780 (Macpherson Range, 2500 ft., Herberton to Tasmania and South and Western Australia).

1109. MACHAERETIS POLEMISTIS Meyr., *Tr.R.S.S.Aust.*, 1902, p. 134 (Brisbane to Gosford).

1110. MACHAERETIS AETHOPIS Meyr., *Tr.R.S.S.Aust.*, 1902, p. 136 (Bunya Mts., Glen Innes, Ebor, Gisborne, Melbourne).

1111. MACHAERETIS ACROXANTHA Meyr., P.L.S.N.S.W., 1884, p. 1066 (Toowoomba to Tasmania).

1112.† MACHAERETIS ANTHERA Meyr., ibid., 1884, p. 1066 (Sydney).

1113. MACHAERETIS PTOCHODES Turn., *Tr.R.S.S.Aust.*, 1917, p. 63 (Brisbane, Esk).

1114. MACHAERETIS ISARITHMA Meyr., ibid., 1884, p. 1063 (Mt. Wellington, 2500 ft.).

1115. MACHAERETIS ACROCOSMA Turn., ibid., 1917, p. 63 (Mt. Tamborine, Macpherson Range).—This species has been accidentally introduced into Britain, and appears to have established itself in Devonshire.

1116. MACHAERETIS XANTHOLOMA Turn., ibid., 1917, p. 64 (Innisfail, Bunya Mts.).

98. Gen. OXYBELES, n.g. (*ὀξυβελης*, sharp-pointed.)

Palpi rather short, slender; second joint not reaching base of antennae; terminal joint one-half, acute. Antennae with basal pecten. Forewings with apex acute; 7 to termen. Hindwings narrowly lanceolate, acute; 3 and 4 separate; cilia 2. Monotypical. An independent derivative of *Coesyra*.

1117. OXYBELES GNOMICA Meyr., ibid., 1884, p. 1062 (Stanthorpe, Sydney).

99. Gen. TACHYSTOLA Meyr. (*Exot. Micro.*, i, p. 241).

Palpi long, curved, ascending, smooth, slender; second joint not reaching base of antennae; terminal joint as long as second. Antennae with basal pecten. Forewings narrow, 7 to termen. Hindwings lanceolate. Type, *T. thiasotis*. Meyrick records one species from India, one from Africa, and three from Australia; but I refer two of the last to *Machaeretis*.

1118. TACHYSTOLA THIASOTIS Meyr., P.L.S.N.S.W., 1884, p. 1060 (Nambour to Castlemaine).

1119. TACHYSTOLA CEROCHYTA, n. sp. (*κηροχυτος*, waxen.)

♂, ♀. 12–14 mm. Head and thorax ochreous-whitish. Palpi whitish; basal two-thirds of outer surface of second joint fuscous. Antennae grey; ciliations in male 1. Abdomen whitish-grey. Legs, anterior pair dark fuscous; middle pair grey; posterior pair whitish. Forewings narrow, suboval, costa moderately arched, apex round-pointed; termen obliquely rounded; shining ochreous-whitish with fuscous markings; a costal streak from base to two-fifths; a spot on two-thirds costa; a subterminal series of dots variably developed; cilia ochreous-whitish. Hindwings broadly lanceolate; whitish; cilia whitish.

North Queensland: Lake Barrine (Atherton Tableland) in September; two specimens.

100. Gen. Spaniacma Meyr. (*Exot. Micro.*, i, p. 129.)

Palpi moderately long; second joint not reaching base of antennae and thickened throughout with dense scales; terminal joint less than one-half, acute. Antennae with strong basal pecten. Abdomen stout, elongate. Forewings rather narrow; 7 to termen. Hindwings lanceolate. Type, *S. bacchias*. An isolated genus of uncertain affinities.

1120. Spaniacma bacchias Meyr., *Exot. Micro.*, i, p. 129 (Darwin).

1121. Spaniacma argyraspis Low., *Tr.R.S.S.Aust.*, 1897, p. 54; Meyr., ibid., 1902, p. 142 (Duaringa, Brisbane).

101. Gen. Antiterpna Meyr. (*Exot. Micro.*, i, p. 274.)

Palpi long, recurved, ascending, smooth, slender; second joint reaching base of antennae; ciliations in male long. Forewings narrow; 7 to termen. Hindwings narrowly lanceolate; 3 and 4 separate; cilia 1. Type, *A. glacialis*. Correlated with *Ocystola*. Four species.

1122.† Antiterpna tephrodes Low., *Tr.R.S.S.Aust.*, 1902, p. 243 (Stawell).

1123.† Antiterpna microphanes Low., ibid., 1902, p. 243 (Stawell, Adelaide).

1124. Antiterpna ptychomochla, n. sp. (*πτυκομοχλος*, with a bar on fold.)

♂. 17–18 mm. Head and thorax white sprinkled with fuscous. Palpi with terminal joint one-half; fuscous, posterior edge white. Antennae grey; ciliations in male 4. Legs fuscous; posterior pair whitish. Forewings narrow, costa slightly arched, apex pointed, termen very oblique; white sparsely sprinkled with blackish; markings blackish; a fine subcostal line from base to costa at one-third; a suffused bar on fold from base to middle; a fine median longitudinal line from middle to three-fourths; cilia white, apices fuscous, on tornus grey. Hindwings and cilia pale grey.

Western Australia: Merredin in September; two specimens.

1125. Antiterpna glacialis Meyr., P.L.S.N.S.W., 1884, p. 1077 (Katoomba, Bathurst, Gisborne, Dimbula, Mt. Lofty).

102. Gen. Opsitycha Meyr. (*Exot. Micro.*, i, p. 249.)

Palpi long, recurved, ascending; second joint exceeding base of antennae, thickened throughout with appressed scales; terminal joint shorter than second, slender, acute. Antennae with basal pecten. Forewings narrow; 7 to termen. Hindwings broadly lanceolate. Type, *O. squalidella*.

1126. Opsitycha squalidella Meyr., P.L.S.N.S.W., 1883, p. 496 (Barrington Tops and Mittagong to Tasmania and Mt. Lofty).

1127. Opsitycha livens, n. sp. (*livens*, leaden-grey.)

♂, ♀. 16–17 mm. Head and thorax grey. Palpi with terminal joint three-fifths; fuscous. Antennae fuscous; ciliations in male two-thirds. Abdomen grey; tuft whitish-ochreous. Legs fuscous-grey. Forewings moderate, costa slightly arched, apex round-pointed, termen oblique; light leaden-grey; a white costal streak from near base to two-thirds; cilia pale grey. Hindwings broadly lanceolate; pale grey; cilia grey-whitish.

South Australia: Cape Jervis in October; two specimens received from Mr. J. O. Wilson.

103. Gen. Ocystola Meyr. (P.L.S.N.S.W., 1884, p. 1057.)

Palpi long, recurved, ascending, smooth; second joint reaching or exceeding base of antennae, slender; terminal joint shorter than second, slender, acute. Antennae with basal pecten; ciliations in male minute, short, moderate or long. Forewings narrow or moderate; 7 to termen. Hindwings broadly or narrowly lanceolate; cilia 1 or less. Type, *O. paulinella*. I include here *Haplodyta* Meyr. and *Laxonoma* Meyr. A large genus which, with *Coesyra*, developed from *Philobota*, but whether by a common stem or separately is uncertain. There are 51 Australian species, and Meyrick has described one from Japan.

1128. Ocystola subtilis, n. sp. (*subtilis*, slender.)

♂. 11–12 mm. Head and thorax white. Palpi with terminal joint two-thirds; white, second joint except apex fuscous. Antennae grey, towards base white; ciliations in male

minute. Abdomen whitish-grey. Legs whitish; anterior pair fuscous. Forewings narrow, costa gently arched, apex pointed, termen very oblique; white with a few ochreous-grey scales; sometimes a faint dot at two-thirds; cilia white. Hindwings rather narrowly lanceolate; whitish; cilia 1, whitish. Characterized by its narrow wings and minute antennal ciliations.

Canberra in February; three specimens.

1129. Ocystola argophanes, n. sp. (*ἀργοφανης*, shining white.)

♂, ♀. 13–14. mm. Head, thorax, and abdomen white. Palpi with second joint exceeding base of antennae, terminal joint two-thirds; whitish. Antennae grey-whitish; ciliations in male 4. Legs grey; posterior pair whitish. Forewings very narrow, costa slightly arched, apex acute, termen extremely oblique; shining white; cilia white. Hindwings narrowly lanceolate; whitish; cilia 1, whitish. The wings are even narrower than in the preceding species, but the antennal ciliations are unusually long.

Queensland: Brisbane in August; Milmerran in October. Western Australia: Tammin in October. Three specimens.

1130. Ocystola linoleuca, n. sp. (*λινολευκος*, linen-white.)

♂. 19 mm. Head and thorax grey-whitish. Palpi with terminal joint two-thirds; white, basal half of external surface of second joint fuscous. Antennae grey, towards base whitish; ciliations in male 4. Abdomen whitish-grey; tuft whitish. Legs whitish; anterior pair fuscous. Forewings moderate, costa gently arched, apex obtuse, termen oblique; white; cilia white, on tornus grey-whitish. Hindwings broadly lanceolate; whitish-grey; cilia whitish. Comparatively broad-winged, forewings spotless white, antennal ciliations long.

Queensland: Macpherson Range (2500 ft.) in December; one specimen.

1131. Ocystola hololeuca Meyr., ibid., 1883, p. 518 = *chalicrata* Turn., *Tr.R.S.S.Aust.*, 1917, p. 60 (Caloundra, Brisbane, Stradbroke I., Toowoomba, Warwick, Milmerran).

1132. Ocystola abductella Meyr. (nec Wlk.), ibid., 1883, p. 517 (Palm Is. and Townsville to Victoria and Mt. Lofty).

1133. Ocystola micropasta, n. sp. (*μικροπαστος*, small sprinkled.)

♂, ♀. 13–16 mm. Head and thorax grey-whitish. Palpi with terminal joint three-fifths; whitish, outer surface of second joint except apex fuscous. Antennae pale grey; ciliations in male one-half. Abdomen dark grey; tuft grey-whitish. Forewings narrow, costa gently arched, apex rounded, termen very obliquely rounded; whitish finely sprinkled with grey; stigmata fuscous, minute or obsolete, first discal at one-third, plical beyond it, second discal at two-thirds; a dot above and between discals; cilia whitish. Hindwings and cilia whitish-grey.

North Queensland: Herberton in September; three specimens.

1134. Ocystola leptostola Meyr., ibid., 1883, p. 517 (Toowoomba to Victoria).

1135. Ocystola vernalis Meyr., ibid., 1883, p. 518 (Sydney).

1136. Ocystola nivea, n. sp. (*niveus*, snow-white.)

♂. 15–16 mm. Head and thorax white. Palpi with terminal joint three-fourths; white, anterior edge fuscous. Antennae whitish, towards apex grey; ciliations in male 2. Abdomen grey-whitish. Legs whitish; anterior pair fuscous. Forewings elongate-oval, costa slightly arched, apex pointed, termen very oblique; shining white; cilia white. Hindwings narrowly lanceolate; grey; cilia 1, grey. Differs from *O. monostropha*, for which it might be mistaken, by the absence of dorsal grey suffusion on forewings, slightly darker hindwings, and especially by the much shorter antennal ciliations (in *monostropha* 5).

Queensland: Brisbane and Warwick in March; two specimens.

1137. Ocystola monostropha Meyr., ibid., 1884, p. 1075 (Marmor, Q., to Victoria and South Australia).

1138. Ocystola lithophanes Meyr., ibid., 1884, p. 1075 (Tasmania).

1139. Ocystola illuta Meyr., ibid., 1884, p. 1074 (Toowoomba to Victoria and South Australia).

1140. Ocystola apathodes Meyr., *Exot. Micro.*, i, p. 240 (Mt. Lofty).

1141. †Ocystola vanescens Meyr., ibid., i, p. 301 (Adelaide).

1142. Ocystola heteropla Meyr., P.L.S.N.S.W., 1885, p. 766 (Bathurst, Colac, Melbourne, Dimbula, Mt. Lofty).

1143. Ocystola thoracta Meyr., ibid., 1885, p. 765 (Macpherson Range to Tasmania; W.A.: Mogumber).

1144. Ocystola ochrogramma Turn., *P.R.S.Tas.*, 1938, p. 93 (Tasmania).

1145. Ocystola capnoessa, n. sp. (*καπνοεις*, smoky.)

♂. 16–17 mm. Head and thorax fuscous. Palpi with terminal joint three-fifths; fuscous. Antennae fuscous; ciliations in male one and a half. Abdomen ochreous-grey; apices of segments whitish; three basal segments fuscous. Legs fuscous with whitish rings. Forewings suboblong, costa slightly arched, apex rounded, termen obliquely rounded; grey, ochreous-tinged, at base suffused with fuscous; stigmata blackish, first discal at two-fifths, plical before it, second discal before two-thirds; sometimes a subterminal series of dots; cilia concolorous. Hindwings broadly lanceolate; grey; cilia grey-whitish.

New South Wales: Maryland (near Stanthorpe) in May and June; two specimens.

1146. Ocystola amphidoxa Meyr., ibid., 1888, p. 1667 (W.A.: Geraldton).

1147. Ocystola perinyctis Meyr., ibid., 1888, p. 1666 (Perth).

1148. Ocystola torosema Meyr., ibid., 1888, p. 1665 (Geraldton).

1149.† Ocystola iochalcha Meyr., ibid., 1885, p. 766 (Mt. Kosciusko; Deloraine, Tas.).

1150. Ocystola paulinella Newm., *Tr.Ent.Soc.*, 1855, p. 297, Pl. 18; Meyr., P.L.S.N.S.W., 1884, p. 1075 (Brisbane to Victoria and South and Western Australia).

1151.† Ocystola holonota Meyr., ibid., 1888, p. 1665 (W.A.: Perth, York).

1152. Ocystola crystallina Meyr., ibid., 1884, p. 1077 (Victoria, Tasmania, South Australia, and Western Australia).

1153.† Ocystola chionea Meyr., ibid., 1884, p. 1076 (Wirrabara, S.A.).

1154.† Ocystola chalchophragma Meyr., ibid., 1888, p. 1680 (W.A.: Perth).

1155. Ocystola xiphomorpha, n. sp. (*ξιφομορφος*, sword-shaped.)

♂. 16–18 mm. Head yellow. Palpi with terminal joint three-fourths; fuscous. Antennae fuscous; ciliations in male 3. Thorax and abdomen fuscous. Legs fuscous; posterior pair pale ochreous. Forewings narrow, costa moderately arched, apex pointed, termen very oblique; yellow; a broad fuscous streak on dorsum; a slender fuscous terminal line; sometimes uniting with dorsal streak; cilia yellowish, on apex and tornus fuscous. Hindwings lanceolate; grey; cilia grey.

Western Australia: Albany in February and March; Denmark in March; Mt. Dale in January; six specimens received from Mr. W. B. Barnard, who has the type.

1156. Ocystola polycapna Turn., *Tr.R.S.S.Aust.*, 1917, p. 61 (Brisbane, Stradbroke I.).

1157. Ocystola basicapna, n. sp. (*βασικαπνος*, with fuscous base.)

♂. 16 mm. Head and thorax grey. Palpi with terminal joint three-fifths; fuscous. Antennae grey; ciliations in male one and a half. Abdomen whitish. Legs whitish; anterior pair fuscous. Forewings narrow, oval, costa moderately arched, apex pointed, termen very oblique; whitish-grey; a broad basal fuscous fascia, its posterior edge suffused; stigmata minute, first discal at one-third, plical before it, second discal at two-thirds, a dot above and beyond first discal; a tornal spot and some terminal dots fuscous; cilia grey-whitish. Hindwings and cilia grey-whitish.

Queensland: Toowoomba in May; one specimen received from Mr. W. B. Barnard.

1158. Ocystola idiosticha Turn., ibid., 1917, p. 63 (Cairns, Brisbane).

1159. Ocystola niphostephana, n. sp. (*νιφοστεφανος*, with snow-white crown.)

♂, ♀. 12–16 mm. Head snow-white; face grey; back of crown brown. Palpi with second joint reaching base of antennae, terminal joint two-thirds; fuscous. Antennae white, annulated except towards base with dark fuscous; ciliations in male one-half. Thorax brown. Abdomen grey. Legs pale ochreous; anterior pair fuscous. Forewings narrow, suboblong, costa gently arched, apex rounded, termen very oblique; uniform pale reddish-brown; cilia concolorous. Hindwings grey; cilia whitish-ochreous, bases grey.

Queensland: Brisbane in March; Crow's Nest near Toowoomba in October. New South Wales: Sydney in January. Four specimens. Type in Coll. Goldfinch.

1160. Ocystola glycydora Turn., ibid., 1917, p. 66 (Brisbane, Sydney, Gisborne).

1161. Ocystola suppressella Wlk., xxix, p. 650; Meyr., P.L.S.N.S.W., 1884, p. 1077 = *tricophora* Turn., ibid., 1917, p. 66 (Rosewood, Tweed Hds., Warwick, Killarney).

1162. Ocystola clethrosema Turn., ibid., 1917, p. 66 (Stanthorpe).

1163. Ocystola paralia Low., *Tr.R.S.S.Aust.*, 1903, p. 225 (Melbourne).

1164. Ocystola episcota Meyr., ibid., 1888, p. 1664 (Stanthorpe to Beaconsfield, Vic.).

1165. Ocystola trilicella Meyr., ibid., 1884, p. 1081 (Tweed Hds. and Stanthorpe to Gisborne and Moe).

1166. Ocystola lochmaea Turn., *Tr.R.S.S.Aust.*, 1917, p. 71 (Atherton Tableland, Mt. Tamborine).

1167. Ocystola callisticha, n. sp. (*καλλιστιχος*, with beautiful lines.)

♂, ♀. 12–14 mm. Head yellow. Palpi with terminal joint three-fourths; yellow, base of second joint fuscous. Antennae dark fuscous annulated with yellow; ciliations in male 3. Thorax and abdomen fuscous; tuft ochreous-grey-whitish. Legs dark fuscous with ochreous-whitish rings. Forewings elongate-oval, costa gently arched, apex pointed, termen very obliquely rounded; deep yellow with fuscous markings; a large spot on base of costa; a narrow fascia from one-third costa to two-fifths dorsum; terminal area fuscous, its anterior edge from two-thirds costa to four-fifths dorsum; cilia fuscous. Hindwings dark grey; cilia grey.

Queensland: Macpherson Range (4,000 ft.) in November; five specimens received from Mr. W. B. Barnard, who has the type.

1168. Ocystola tyrianthina, n. sp. (*τυριανθινος*, purple-flowered.)

♂, ♀. 13–14 mm. Head ochreous-yellow. Palpi with terminal joint two-thirds; pale yellow, external surface of second joint except apex fuscous. Antennae grey; ciliations in male one and a half. Thorax fuscous. Abdomen grey; tuft pale ochreous. Legs fuscous with pale ochreous rings; posterior pair mostly pale ochreous. Forewings dilated posteriorly, costa gently arched, apex pointed, termen straight, moderately oblique; yellow; a small fuscous basal fascia; a fuscous costal streak to beyond middle; a broad terminal purple-fuscous fascia; cilia fuscous, apices ochreous-whitish except on tornus. Hindwings broadly lanceolate; grey; cilia grey.

Queensland: Talwood in December; two specimens received from Mr. W. B. Barnard, who has the type.

1169. Ocystola oxytona Turn., P.L.S.N.S.W., 1916, p. 257 (Ebor).

1170.† Ocystola pyramis Meyr., ibid., 1884, p. 1073 (Sydney, Katoomba).

1171. Ocystola euanthes Meyr., ibid., 1884, p. 1072 = *hemidesma* Low., ibid., 1897, p. 268 = *pachythrix* Turn., *Tr.R.S.S.Aust.*, 1917, p. 62 (Gisborne, Beaconsfield, Adelaide, Wirrabara).

1172. Ocystola proselia Turn., ibid., 1917, p. 762 (Macpherson Range, Killarney, Stanthorpe).

1173. Ocystola oridroma, n. sp. (*ὀρειδρομος*, frequenting the mountains.)

♂. 13–15 mm. Head orange. Palpi with second joint reaching base of antennae, terminal joint four-fifths; yellowish, terminal joint and an anterior subapical dot on second joint fuscous. Antennae dark fuscous; basal joint orange; ciliations in male two and a half. Thorax dark fuscous. Abdomen dark fuscous; beneath yellowish. Legs fuscous; middle and posterior femora and posterior tibiae partly yellowish. Forewings narrow, not dilated, costa gently arched, apex rounded, termen oblique; dark fuscous; a broad sub-basal fascia extending from near base to one-third, bright yellow, slightly broader on dorsum; cilia dark fuscous. Hindwings lanceolate; fuscous; cilia fuscous.

The antennal pecten is weak in this species. It resembles *O. proselia* Turn., but in this the apex of the forewings is acute and the basal fascia is prolonged along costa to middle. All my examples are of the male sex, which flies in the daytime.

Queensland: Macpherson Range (3500–4000 ft.) from December to March; 16 specimens. I did not find it at lower levels.

1174. Ocystola hemimelas, n. sp. (*ἡμιμελας*, half black.)

♂. 13 mm. Head yellowish. Palpi with terminal joint two-thirds; pale fuscous. Antennae blackish; ciliations in male 6. Thorax and abdomen blackish. Legs fuscous. Forewings narrow, costa straight, apex pointed, termen straight, very oblique; yellow; a narrow basal fascia dark fuscous; apical half of wing dark fuscous, its anterior edge straight, sharply defined; cilia dark fuscous. Hindwings narrowly lanceolate; dark fuscous; cilia dark fuscous.

Western Australia: Perth in October; one specimen.

1175. Ocystola chrysopis Meyr., *Tr.R.S.S.Aust.*, 1902, p. 135 (Sydney).

1176. Ocystola misthota Meyr., ibid., 1902, p. 135 (Atherton Tableland, Sydney).

1177. Ocystola placoxantha Meyr., P.L.S.N.S.W., 1884, p. 1072 (Toowoomba, Bathurst).

1178. Ocystola mesoxantha Meyr., ibid., 1884, p. 1073 (Brisbane, Toowoomba, Warwick, Sydney).

(Gen. Parocystola Turn.).

This genus was founded for *P. leucospora* Turn. Unfortunately I misconceived its true position, for I am now convinced that it is by no means closely allied to *Ocystola*, but belongs to the *Machimia–Heliocausta* group, which will be dealt with later in this series. In wing-shape it approaches most nearly *Zonopetala viscata* Meyr. The palpi have the second joint reaching base of antennae, the terminal joint shorter than second, and the antennae are without basal pecten (rarely with a solitary scale or two); characters inconsistent with Meyrick's definition in the Genera Insectorum. In addition the hindwings have short cilia and 5 curved and approximated to 4 at origin.

The other species placed by Meyrick in this genus I have transferred to other genera (*Machaeretis*, *Coesyra*, and *Philobota*).

104. Gen. Crepidosceles Meyr. (P.L.S.N.S.W., 1884, p. 1055.)

Palpi with second joint not or just reaching base of antennae, moderately slender, smooth; terminal joint shorter than second, slender, acute. Antennae with basal pecten. Anterior tibiae and tarsi dilated with dense scales. Forewings with 7 to termen. Hindwings rather narrowly elongate-ovate; neuration normal. Type *C. iostephana*. A development of *Philobota*. There are 6 species.

1179. Crepidosceles habrodelta Low., ibid., 1897, p. 20 (Stanthorpe, Katoomba, Gisborne).

1180. Crepidosceles miltotypa, n. sp. (*μιλτοτυπος*, reddish-marked.)

♂. 16–18 mm. Head white; side-tufts dark red. Palpi smooth, slender, acute, terminal joint less than one-half; white. Antennae white; ciliations in male 5. Thorax white, anterior margin dark red. Abdomen whitish-grey. Legs ochreous-whitish; anterior pair dark red. Forewings narrow, costa straight except at base and apex, apex pointed, termen very oblique; white with red markings; a spot on base of costa and another at one-fifth; a broad irregular partly interrupted streak containing some fuscous scales from base along fold to above tornus; an apical spot and a series of terminal dots; cilia pale red, bases whitish. Hindwings whitish-grey; cilia whitish.

♀. 11–16 mm. Head and thorax grey. Palpi with second joint pale red. Forewings without costal, apical, and terminal spots; subdorsal streak darker.

Queensland: Injune in April; five specimens received from Mr. W. B. Barnard, who has the type.

1181. Crepidosceles iostephana Meyr., P.L.S.N.S.W., 1884, p. 1056 = *iodeta* Turn., *Tr.R.S.S.Aust.*, 1898, p. 211 (Brisbane, Sydney).

1182. Crepidosceles exanthema Meyr., ibid., 1884, p. 1057 (Brisbane, Toowoomba, Melbourne; Quorn, S.A.).

1183. Crepidosceles timalphes Turn., *Tr.R.S.S.Aust.*, 1917, p. 70 (Stanthorpe, Toowoomba, Gisborne, Beaconsfield, Castlemaine).

1184. Crepidosceles butyrea, n. sp. (*βουτυρεος*, butter-coloured.)

♂, ♀. 12–14 mm. Head pale yellow. Palpi with terminal joint four-fifths; pale yellow, outer surface of second joint except apex fuscous. Antennae grey; ciliations in

male 2. Thorax fuscous; apices of tegulae and a posterior spot whitish. Abdomen ochreous-fuscous. Legs fuscous; posterior pair ochreous-whitish. Forewings rather narrow, costa moderately arched, apex pointed, termen very oblique; pale yellow; costal edge towards base fuscous; a broad purple-fuscous terminal band, its anterior edge from three-fifths costa to two-thirds dorsum, inwardly curved, fuscous; cilia fuscous, apices pale yellow except towards tornus. Hindwings and cilia dark grey.

Queensland: Rosewood and Warwick in October; three specimens.

105. Gen. HIPPOMACHA Meyr. (*Exot. Micro.*, i, p. 244.)

Palpi with second joint not reaching base of antennae, slender, smooth; terminal joint usually one-fourth, at most one-third, slender, acute. Antennae with basal pecten. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Type *H. callista*. Nine species.

Larva in a portable case formed of a single cylindrical hollowed twig.

1185. HIPPOMACHA CALLISTA Meyr., P.L.S.N.S.W., 1884, p. 1067 (Stanthorpe, Toowoomba, Sydney, Gisborne).

1186. HIPPOMACHA INVALIDA, n. sp. (*invalidus*, weak.)

♂. 16 mm. Head and thorax pale brown. Palpi with terminal joint one-third; pale brown. Antennae brown; ciliations in male 3. Abdomen grey. Legs fuscous; posterior pair ochreous. Forewings narrow, dilated posteriorly, costa gently arched, apex pointed, termen oblique; pale brown; cilia pale fuscous. Hindwings pale ochreous; a small pale fuscous apical blotch; cilia pale fuscous.

Queensland: Brisbane in September; one specimen.

1187. HIPPOMACHA HELIOTRICHA Low., *Tr.R.S.S.Aust.*, 1904, p. 168 (Hobart).

1188. HIPPOMACHA PYROCHRYSA Meyr., P.L.S.N.S.W., 1888, p. 1663 (Brisbane, Sydney, Gisborne, Beaconsfield).

1189. HIPPOMACHA OXYPTERA Low., *Tr.R.S.S.Aust.*, 1894, p. 101 (Stawell).

1190. HIPPOMACHA RELUCENS Meyr., *Exot. Micro.*, i, p. 116 (Gisborne).

1191. HIPPOMACHA HEMICALYPTA Meyr., P.L.S.N.S.W., 1884, p. 1061 (Tyringham, N.S.W.; Melbourne, Gisborne).

1192.† HIPPOMACHA THYMODES Meyr., ibid., 1884, p. 1061 (Quorn, S.A.).

1193. HIPPOMACHA HALATA Meyr., *Exot. Micro.*, i, p. 117 (Gisborne).

106. Gen. HEMIBELA Turn. (*Tr.R.S.S.Aust.*, 1914, p. 136.)

Palpi with second joint not reaching base of antennae, moderately slender, smooth; terminal joint minute. Antennae with basal pecten. Forewings with 7 to termen. Hindwings broadly ovate; neuration normal. Monotypical. Closely allied with *Hippomacha* and with identical larval case. Differs only in the minute terminal joint of palpi and the broader hindwings.

1194. HEMIBELA TYRANNA Meyr., ibid., 1884, p. 1066 = *trispora* Turn., *Tr.R.S.S.Aust.*, 1894, p. 136 (Brisbane, Quorn; Cunderdin, W.A.).

107. Gen. PERIORYCTA Meyr. (*Exot. Micro.*, ii, p. 511.)

Tongue weakly developed. Palpi with second joint not reaching base of antennae, thickened with appressed scales; terminal joint shorter than second, slender, acute. Antennae with basal pecten. Forewings with 3 absent, 7 to termen. Hindwings elongate-ovate; 4 absent. Monotypical.

1195. PERIORYCTA EUCRAERA Turn., *Tr.R.S.S.Aust.*, 1917, p. 64 = *stelidias* Meyr., l.c., ii, p. 511 (Mackay, Dalby, Warwick, Milmerran). Lower's localities are not always reliable.

108. Gen. SYSCALMA Meyr. (*Exot. Micro.*, ii, p. 381.)

Tongue well developed. Palpi with second joint not reaching base of antennae, smooth, slender; terminal joint shorter than second, slender, acute. Antennae without basal pecten. Forewings with 7 to termen, 10 absent. Hindwings elongate-ovate; neuration normal. Type *S. prymnaea*.

1196. SYSCALMA PRYMNAEA Meyr., *Exot. Micro.*, ii, p. 381 (Dalby, Chinchilla, Q.).

1197. Syscalma stenoxantha, n. sp. (*στενοξανθος*, narrowly yellow.)

♂. 13 mm. Head pale yellow. Palpi with second joint not reaching base of antennae, terminal joint 1; pale yellow, second joint with base and a subapical ring fuscous. Antennae fuscous; ciliations in male 2½. Thorax and abdomen dark fuscous. Legs fuscous with ochreous rings; posterior pair mostly ochreous. Forewings moderate, costa moderately arched, apex rounded, termen obliquely rounded; dark fuscous; a narrow yellow antemedian transverse fascia; cilia dark fuscous. Hindwings ovate-lanceolate; bronzy-grey; cilia grey.

North Queensland: Cape York in May; one specimen received from Mr. W. B. Barnard.

109. Gen. Calypta, n.g. (*καλυπτος*, veiled.)

Head with long hairs from crown projecting downwards over face. Tongue rudimentary. Palpi rather short, slightly curved, ascending, smooth; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae with basal joint stout, pecten broad and dense, covering most of eye. Forewings with 7 and 8 long-stalked separating close to apex. Hindwings elongate-ovate. A specialized derivative of *Coesyra*.

1198. Calypta acerasia, n. sp. (*ἀκηρασιος*, pure.)

♂. 15 mm. Head and thorax white. Palpi with terminal joint one-half; white. Antennae white; ciliations in male one and a half. Abdomen whitish-grey. Legs white; anterior pair fuscous. Forewings suboval, costa strongly arched, apex pointed, termen very oblique; shining white; cilia white. Hindwings and cilia whitish-grey.

Queensland: Duaringa in November; two specimens received from Mr. W. B. Barnard, who has the type.

110. Gen. Sphaerelictis Meyr. (*Exot. Micro.*, iii, p. 102.)

Tongue rudimentary or absent. Palpi with second joint not reaching base of antennae, smooth, slender; terminal joint very short, slender, acute. Antennae without basal pecten. Anterior tibiae and tarsi short and thickened with appressed scales; the former expanded at apex. Forewings with 7 to termen, 9 separate, stalked with 10, or rarely stalked with 7, 8. Hindwings broadly ovate; neuration normal. Type, *S. dorothea* Meyr. from India. There is a second Indian species. The variability of 9 of forewings is extraordinary.

1199. Sphaerelictis niphodisca, n. sp. (*νιφοδισκος*, with snow-white discs.)

♂. 18 mm. Head whitish. Palpi with terminal joint one-third; pale ochreous, terminal joint whitish. Antennae fuscous; ciliations in male one and a half. Thorax yellow; patagia fuscous-brown. Abdomen brownish; tuft ochreous. Legs whitish; anterior pair ochreous-fuscous. Forewings elongate-triangular, costa straight except at base and apex, apex subrectangular, termen straight, slightly oblique; 9 and 10 long-stalked; pale yellow; markings snow-white edged with fuscous and partly surrounded by reddish-ochreous suffusion; a large circular sub-basal dorsal spot; a small triangle at tornus surmounted by an almost circular spot in mid-disc; cilia pale yellow, on tornal spot white, above this reddish-fuscous. Hindwings grey; cilia whitish.

Differs from *S. hepialella* in the whitish head and two circular spots on forewings.

North Queensland: Herberton in January; two specimens received from Mr. F. P. Dodd. One of these is in Coll. Lyell.

1200. Sphaerelictis hepialella Wlk., xxx, p. 1033; Turn., *Tr.R.S.S.Aust.*, 1917, p. 75; Meyr., *Gen. Ins.*, Oecoph., Pl. iii, f. 57 (Darwin, Cairns, Townsville, Brisbane, Toowoomba, Dalby, Katoomba).

This species shows some sexual dimorphism. The male is wholly reddish or mostly reddish with some yellow suffusion; the female wholly yellow or with some reddish suffusion, but in one example is mostly reddish. More remarkable is the variability of vein 9 of the forewings. In six male examples this vein is present, usually separate, more rarely connate with 7, 8. In ten female examples it is separate or connate in four, stalked with 7, 8 in two, and long-stalked with 10 in four. None were observed with 9 absent or short-stalked with 10, and in every case the neuration was similar on both sides.

The larvae feed on *Eucalyptus* saplings, constructing spirally folded cases of leaf fragments resembling in shape the shells of snails.

111. Gen. Aristeis Meyr. (P.L.S.N.S.W., 1884, p. 762.)

Tongue developed. Palpi with second joint not reaching base of antennae, moderately thickened with appressed scales; terminal joint half second, slender, acute. Antennae without basal pecten; ciliations in male long and dense. Anterior tibiae and tarsi short and thickened with appressed scales, the former expanded at apex. Forewings with 7 to termen. Hindwings as broad as forewings; neuration normal. Probably monotypical.

1201. Aristeis chrysoteuches Meyr., l.c., 1884, p. 762 (Tweed Hds. to Hobart).

112. Gen. Olbonoma Meyr. (*Exot. Micro.*, i, p. 244.)

Palpi with second joint not or scarcely reaching base of antennae, smooth, slender; terminal joint shorter than second, slender, acute. Antennae with basal pecten. Forewings with 7 to termen. Hindwings elongate ovate; 6 and 7 approximated at base. Type, *O. callopistis* Meyr.

1202. Olbonoma callopistis Meyr., *Exot. Micro.*, i, p. 116 (Darwin).

1203. Olbonoma poliophracta, n. sp. (πολιοφρακτος, grey-edged.)

♂. 14 mm. Head and thorax ochreous-whitish. Palpi with terminal joint three-fourths; ochreous-whitish. Antennae grey; ciliations in male two-thirds. Abdomen grey. Legs ochreous-whitish, anterior pair fuscous. Forewings with costa strongly arched, apex round-pointed, termen obliquely rounded; ochreous-whitish; in one example a slender inwardly curved grey line from four-fifths costa to tornus; terminal edge grey; cilia grey. Hindwings and cilia grey-whitish.

Queensland: Stradbroke I. in December; Stanthorpe in January; three specimens.

1204. Olbonoma staitina, n. sp. (σταιτινος, floury.)

♂. 11 mm. Head white. Palpi with terminal joint three-fourths; white, second joint fuscous towards base. Antennae grey; ciliations in male one and a quarter. Thorax fuscous; posterior edge white. Abdomen grey; tuft whitish. Legs whitish; anterior pair grey. Forewings suboval, costa moderately arched, apex round-pointed, termen oblique; white; a fuscous dot on base of costa; cilia white. Hindwings and cilia whitish-grey.

Queensland: Bundaberg in September; one specimen.

113. Gen. Coesyra Meyr. (P.L.S.N.S.W., 1884, p. 763.)

Palpi with second joint not reaching base of antennae, slender or somewhat thickened with appressed scales; terminal joint shorter than second, slender, acute. Antennae with basal pecten; ciliations in male long, moderate, short, or minute. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *C. cyclotoma*. A derivative of *Philobota*, from which it is sometimes not easily distinguished. In its turn it has given rise to *Machaeretis* and other related genera. There are 110 Australian species. Meyrick has described also one from India and two from Africa.

1205.† Coesyra thoenatica Meyr., *Exot. Micro.*, ii, p. 312 (Brisbane).

1206. Coesyra pyrota Meyr., P.L.S.N.S.W., 1888, p. 1604; Gen. Oecophor., Pl. 4, f. 61 (W.A.: York, Waroona, Tammin).

1207. Coesyra amydrophanes, n. sp. (ἀμυδροφανης, dull-looking.)

♂, ♀. 19–20 mm. Head pale greyish-ochreous. Palpi with second joint thickened towards apex, terminal joint three-fourths; fuscous. Antennae grey; ciliations in male 3, in female one-half. Thorax fuscous. Abdomen grey. Legs fuscous; posterior pair ochreous-whitish. Forewings elongate, not dilated, apex rounded, termen oblique; grey, in female ochreous-tinged; stigmata and some scattered scales fuscous; first discal at one-third, plical beyond it, second discal at two-thirds, double, a dot above and beyond plical; cilia grey. Hindwings whitish-ochreous, towards apex suffused with grey; cilia whitish-ochreous, on apex grey.

New South Wales: Glen Innes in March; Armidale in December; two specimens.

1208. Coesyra aeglitis, n. sp. (*αἰγλιτις*, brilliant.)

♂. 14–16 mm. Head and thorax fuscous. Palpi with terminal joint three-fifths; fuscous. Antennae fuscous; in male with joints dilated at apices, ciliations two-thirds. Abdomen fuscous. Legs fuscous with whitish rings. Forewings narrow, costa gently arched, apex round-pointed, termen very oblique; pale grey densely sprinkled with dark fuscous; stigmata dark fuscous, obscure, first discal at one-third, plical beyond it, second discal before two-thirds; a dot above tornus; cilia dark fuscous. Hindwings bright orange; some fuscous suffusion at apex; cilia fuscous.

New South Wales: Gosford in October; two specimens received from Mr. G. M. Goldfinch, who has the type.

1209. Coesyra susanae Low., P.L.S.N.S.W., 1900, p. 44 (Broken Hill, Birchip).

1210. Coesyra olympias Low., ibid., 1899, p. 107 (Broken Hill).

1211. Coesyra perigypsa Low., *Tr.R.S.S.Aust.*, 1901, p. 88 (Broken Hill).

1212. Coesyra melanthes Low., P.L.S.N.S.W., 1899, p. 108; = *rhiphidura* Meyr., *Exot. Micro.*, i, p. 133 (Broken Hill, Birchip).

1213. Coesyra crassinervis Low., ibid., 1900, p. 44 (Broken Hill).

1214. Coesyra siligmias Low., ibid., 1899, p. 107 (Broken Hill).

1214*a*. Coesyra zalias Low., P.L.S.N.S.W., 1889, p. 107 (Broken Hill, Birchip).

1215. Coesyra paragypsa Low., ibid., 1900, p. 412 (Birchip, Adelaide, Pinnaroo).

1216.† Coesyra apothyma Meyr., ibid., 1884, p. 787 (Petersburg, S.A.).

1217. Coesyra tapinophanes, n. sp. (*ταπεινοφανης*, of humble appearance.)

♂. 20–24 mm. Head, thorax, and abdomen pale grey. Palpi with terminal joint three-fourths; whitish. Antennae pale grey; ciliations in male 1. Legs grey; posterior pair whitish. Forewings elongate, not dilated, costa almost straight, apex pointed, termen strongly oblique; whitish finely sprinkled with grey; cilia whitish with grey points. Hindwings grey-whitish; cilia whitish.

Queensland: Cunnamulla in April; three specimens.

1218. Coesyra xanthocoma Low., P.L.S.N.S.W., 1899, p. 110 (Broken Hill).

1219. Coesyra phoenopis, n. sp. (*φοινωπις*, reddish.)

♀. 15 mm. Head ochreous-whitish. Palpi with terminal joint one-half; grey, base of second joint whitish. Antennae grey. Thorax white with median and lateral fuscous stripes. Abdomen pale grey. Legs ochreous-whitish; anterior pair fuscous. Forewings narrow, dilated posteriorly, costa slightly arched, apex pointed, termen oblique; pale reddish suffused with whitish towards base; a whitish subcostal streak to middle; another on fold from base to tornus; a broader median streak from one-fifth to four-fifths; interrupted by fuscous dots at two-fifths and two-thirds; a fuscous terminal line preceded by a pale line; cilia reddish, on tornus whitish-grey. Hindwings grey; cilia whitish-grey.

Western Australia: Busselton in February; Denmark in March; two specimens received from Mr. W. B. Barnard.

1220. Coesyra aclea Meyr., P.L.S.N.S.W., 1882, p. 456 (Beaconsfield, Vic.; Tasmania).

1221. Coesyra phaulopis Turn., *Tr.R.S.S.Aust.*, 1917, p. 64 (Brisbane).

1222. Coesyra byssodes, n. sp. (*βυσσωδης*, linen-white.)

♂. 18 mm. Head and thorax white. Palpi with terminal joint 1; whitish, second joint fuscous towards base. Antennae grey, base white; ciliations in male 1½. Abdomen pale grey. Legs fuscous; posterior pair whitish. Forewings narrow, costa strongly arched, apex pointed, termen very oblique; white finely sprinkled with grey; a minute grey discal dot at three-fifths and another at two-thirds; cilia white. Hindwings and cilia whitish.

Queensland: Rockhampton in September; one specimen.

1223. Coesyra cretea, n. sp. (*creteus*, chalky.)

♂. 18–20 mm. Head and thorax grey-whitish. Palpi with second joint not reaching base of antennae, terminal joint one-third; whitish. Antennae whitish; ciliations in male 3. Abdomen and legs whitish. Forewings moderately broad, costa moderately arched, apex pointed, termen oblique; grey-whitish; discals minute or obsolete, fuscous, first discal at one-third, plical beneath it, second discal at three-fifths; a few scattered

fuscous scales; an interrupted fuscous terminal line; cilia grey-whitish. Hindwings ovate; white; cilia white.

Queensland: Brisbane and Tweed Heads in September. New South Wales: Sydney in September. Five specimens.

1224. Coesyra holodryas Low., P.L.S.N.S.W., 1899, p. 110 (Broken Hill).

1225. Coesyra torpens Meyr., *Exot. Micro.*, ii, p. 382 (Sydney).

1226. Coesyra dictyodes Meyr., P.L.S.N.S.W., 1888, p. 1662 (Mt. Kosciusko, 7000 ft.).

1227. Coesyra xantholopha, n. sp. (ξανθολοφος, with yellowish tuft.)

♂. 20 mm. Head whitish-brown. Palpi with terminal joint three-fifths; whitish-brown. Antennae whitish-brown annulated with dark fuscous; ciliations in male 3. Thorax pale fuscous. Abdomen brown; tuft whitish-brown. Legs whitish-ochreous; anterior pair fuscous. Forewings suboval, costa moderately arched, apex pointed, termen strongly oblique; brown-whitish with slight pale fuscous irroration; stigmata very obscure, first discal at one-third, plical beyond it, second discal before two-thirds; cilia brown-whitish. Hindwings ovate; a strong pencil of long ochreous hairs from beneath base; grey-whitish; cilia grey-whitish.

Although very obscure, the male should be easily recognized by the long pencil of hairs on the underside. It arises from the side of the thorax beneath the origin of the hindwing.

Queensland: Macpherson Range (2500 ft.) in open forest in November; one specimen.

1228. Coesyra plectanora Turn., *P.R.S.Tas.*, 1926, p. 148 (Mt. Wellington 2500 ft.).

1229.† Coesyra phaeodesma Meyr., *Exot. Micro.*, i, p. 115 (Cairns).

1230. Coesyra gephyrota Meyr., P.L.S.N.S.W., 1884, p. 788 (Brisbane to Tyringha, N.S.W.).

1231.† Coesyra paraderces Meyr., ibid., 1888, p. 1659 (N.S.W.?).

1232. Coesyra hemiphragma Meyr., ibid., 1888, p. 1659; = *sororia* Turn., *Tr.R.S.S.Aust.*, 1898, p. 210 (Nambour to Sydney).

1233.† Coesyra melanoscia Meyr., ibid., 1888, p. 1660 (W.A.: Albany).

1234.† Coesyra phlopsamma Meyr., ibid., 1883, p. 379 (Wallaroo, S.A.).

1235. Coesyra macrotricha Turn., ibid., 1917, p. 65 (Brisbane).

1236. Coesyra achranta Turn., *Tr.R.S.S.Aust.*, 1917, p. 74 (Tenterfield).

1237. Coesyra melliflua Meyr., P.L.S.N.S.W., 1884, p. 781 (Townsville, Duaringa, Brisbane, Tenterfield).

1238.† Coesyra xuthoterma Meyr., *Exot. Micro.*, ii, p. 311 (Brisbane).

1239. Coesyra protosticha Meyr., ibid., 1884, p. 1071; = *asema* Turn., *Tr.R.S.S.Aust.*, 1917, p. 74.—In this species the markings on the forewings are usually obsolete, and it may then be distinguished from the preceding by the longer antennal ciliations of the male (2½). (Duaringa, Stradbroke I., Tweed Hds., Toowoomba, Charleville).

1240. Coesyra panxantha Meyr., ibid., 1884, p. 784 (Sydney, Bulli, Katoomba, Mt. Wilson).

1241.† Coesyra colonaea Meyr., *Tr.R.S.S.Aust.*, 1902, p. 139 (Bathurst).

1242. Coesyra panchrysa Meyr., P.L.S.N.S.W., 1884, p. 766 (Sydney, Mittagong).

1243. Coesyra cerochyta Turn., *P.R.S.Tas.*, 1938, p. 93 (Mt. Wellington 2500 ft.).

1244. Coesyra ochrocirrha Turn., *P.R.S.Tas.*, 1926, p. 148 (Cradle Mt. 3000 ft., Gordon R.).

1245.† Coesyra amylodes Meyr., ibid., 1884, p. 784 (Murrurundi).

1246. Coesyra monodyas Meyr., ibid., 1884, p. 1047 (Herberton, Tweed Hds. to Tasmania).

1247. Coesyra allocoma Meyr., ibid., 1884, p. 1047 (Milmerran to Victoria).

1248. Coesyra epicona Meyr., ibid., 1884, p. 1046 (Sea Lake, Vic.; Petersburg and Ardrossan, S.A.; York, W.A.).

1249. Coesyra tanythrix Turn., P.L.S.N.S.W., 1914, p. 557 (Ebor).

1250. Coesyra leptospila Meyr., ibid., 1888, p. 1654 (Cape York to Brisbane).

1251.† Coesyra vegrandis Meyr., ibid., 1884, p. 790 (Sydney).

1252.† Coesyra arenivaga Meyr., ibid., 1884, p. 790 (Sydney).

1253. Coesyra haplophara Turn., ibid., 1915, p. 192 (Ebor).

1254. Coesyra enoplia Meyr., ibid., 1884, p. 1069 (Pt. Lincoln).

1255. Coesyra malacella Meyr., ibid., 1884, p. 1064 = *callixantha* Meyr., ibid., 1888, p. 1663 = *holoxantha* Meyr., *Tr.R.S.S.Aust.*, 1902, p. 136 (Nambour to Tasmania).

1256.† Coesyra oxyxantha Meyr., *Exot. Micro.*, i, p. 245 (Bulli).

1257. Coesyra chrysoptera, n. sp. (*χρυσοπτερος*, golden-winged.)

♂. 14 mm. Head and thorax orange-yellow. Palpi with terminal joint one-half; yellow. Antennae grey; ciliations in male 1. Abdomen pale grey; tuft whitish. Legs grey; posterior pair whitish. Forewings narrow, suboval, costa moderately arched, apex pointed, termen very oblique; orange-yellow; cilia pale grey. Hindwings and cilia pale grey.

Western Australia: Kalamunda near Perth in December; one specimen received from Mr. W. B. Barnard.

1258. Coesyra galbanea Meyr., ibid., i, p. 115 (Gisborne).

1259.† Coesyra permeata Meyr., ibid., i, p. 117 (Cairns).

1260.† Coesyra austalea Meyr., P.L.S.N.S.W., 1884, p. 789 (Bulli).

1261. Coesyra synoeches Turn., ibid., 1914, p. 558 (Ebor).

1262.† Coesyra drymelanthes Low., *Tr.R.S.S.Aust.*, 1907, p. 116 (Broken Hill).

1263. Coesyra polyzona, n. sp. (*πολυζωνος*, much banded.)

♂, ♀. 15–18 mm. Head yellow. Palpi with terminal joint one-third; whitish, base of external surface of second joint fuscous. Antennae grey; ciliations in male 1. Thorax yellow; anterior edge fuscous. Abdomen grey; tuft whitish-ochreous. Legs fuscous; posterior pair whitish-ochreous. Forewings with costa moderately arched, apex round-pointed, termen obliquely rounded; yellow; markings fuscous; a narrow sub-basal outwardly curved fascia; a second fascia from two-fifths costa to mid-dorsum; a third from four-fifths costa to tornus connected with second in middle; a fourth terminal, not reaching tornus; cilia yellow, on tornus fuscous. Hindwings and cilia grey.

Queensland: Stanthorpe in January, February, and March; six specimens received from Mr. W. B. Barnard, who has the type.

1264. Coesyra basilica Meyr., ibid., 1884, p. 770 (Sydney, Melbourne, Hobart; Wallaroo, S.A.; Perth, W.A.).

1265. Coesyra phricomita, n. sp. (*φρικομιτος*, with rippled thread.)

♂. 14–18 mm. Head yellow. Palpi with terminal joint two-thirds; ochreous-whitish, second joint sometimes fuscous at base, terminal joint with sub-basal and subapical fuscous rings. Antennae grey; ciliations in male 1½. Thorax yellow; anterior edge fuscous. Abdomen grey. Legs fuscous with ochreous-whitish rings; posterior pair ochreous-whitish. Forewings with costa strongly arched, apex round-pointed, termen oblique; yellow; markings fuscous; a costal streak from base to one-fifth; a finely but irregularly dentate line from one-third costa to one-third dorsum; a curved line from four-fifths costa to four-fifths dorsum; a triangular subapical spot continued as a line on termen to tornus; cilia yellow, on tornus fuscous. Hindwings and cilia grey.

Queensland: Toowoomba in October and November; Stanthorpe in January; four specimens received from Mr. W. B. Barnard, who has the type. New South Wales: Murrurundi (Dr. B. L. Middleton).

1266. Coesyra epistrepta, n. sp. (*ἐπιστρεπτος*, admirable.)

♂, ♀. 10–12 mm. Head yellow. Palpi with terminal joint two-thirds; yellow. Antennae grey; ciliations in male 2. Thorax yellow with an anterior fuscous spot. Abdomen fuscous; tuft whitish-ochreous. Legs fuscous; posterior pair ochreous-whitish. Forewings with costa gently arched, apex rounded, termen obliquely rounded; yellow; a fuscous line from one-third costa to one-fourth dorsum, outwardly curved above middle; a violet apical blotch edged by a fuscous line from five-sixths costa to tornus; cilia yellow, on tornus fuscous. Hindwings and cilia grey.

Western Australia: Albany in February and March; two specimens received from Mr. W. B. Barnard, who has the type.

1267. Coesyra distephana Meyr., ibid., 1884, p. 768 (Brisbane to Melbourne, Mt. Lofty, and Western Australia).

1268. Coesyra translatella Wlk., xxx, p. 1029 = *iozona* Meyr., ibid., 1884, p. 769 = *dicoela* Turn., *Tr.R.S.S.Aust.*, 1896, p. 29 (Herberton, Brisbane to Melbourne and Hobart).

1269. Coesyra miltozona Low., ibid., 1901, p. 93 (Darwin, Townsville).

1270. Coesyra ophthalmica Meyr., P.L.S.N.S.W., 1884, p. 775 (Mt. Tamborine to Hobart).

1271. Coesyra anthodora Meyr., ibid., 1884, p. 769 (Mt. Tamborine to Hobart).

1272.† Coesyra tricoronata Meyr., *Exot. Micro.*, ii, p. 312 (W.A.: Margaret R.).

1273. Coesyra thermistis Meyr., P.L.S.N.S.W., 1888, p. 1654 (Atherton, Duaringa).

1274. Coesyra aspasia Meyr., ibid., 1884, p. 783 (Pt. Lincoln, Albany, Perth, Geraldton).

1275. Coesyra paraclista Meyr., *Exot. Micro.*, i, 116 (Cairns, Nambour, Mt. Tamborine, Killarney).

1276. Coesyra iphia, n. sp. (*ἰφιος*, handsome.)

♂, ♀. 18–24 mm. Head yellow. Palpi with terminal joint two-thirds, yellowish with some fuscous irroration. Antennae grey; ciliations in male 1. Thorax yellow with a pale fuscous anterior spot. Abdomen ochreous-grey-whitish; tuft whitish-ochreous. Legs fuscous; posterior pair whitish-ochreous. Forewings narrow, costa slightly arched, apex rounded, termen obliquely rounded; yellow; an inwardly curved crescent from apex to dorsum at three-fourths, very thin towards apex, thickening towards dorsum, violet edged with fuscous anteriorly; cilia yellow, bases tinged violet. Hindwings and cilia pale grey.

Western Australia: Busselton in February; eight specimens received from Mr. W. B. Barnard, who has the type. South Australia: two examples from Adelaide (J. O. Wilson) are probably the same species, but have the subterminal crescent broader, more fuscous, and the cilia also partly or wholly fuscous.

1277. Coesyra pleurophaea, n. sp. (*πλευροφαιος*, with dusky costa.)

♂. 14 mm. Head pale yellow. Palpi with terminal joint two-thirds; pale yellow, basal half of outer surface of second joint fuscous. Antennae fuscous; ciliations in male 4. Thorax fuscous, anterior edge yellow. Abdomen fuscous. Legs fuscous; posterior pair whitish-ochreous. Forewings dilated posteriorly, costa moderately arched, apex round-pointed, termen oblique; pale yellow with fuscous markings; a broad costal streak from base narrowing to a point at three-fourths; a narrow inwardly-curved fascia from four-fifths costa to tornus; cilia fuscous. Hindwings and cilia grey.

North Queensland: Gordonvale near Cairns; type in Coll. Lyell.

1278. Coesyra thiodes Turn., *Tr.R.S.S.Aust.*, 1917, p. 74 (W.A.: Cunderdin, Mogumber).

1279.† Coesyra asthenopis Meyr., P.L.S.N.S.W., 1888, p. 1658 (W.A.: Carnarvon).

1280. Coesyra polyphila Turn., *P.R.S.Tas.*, 1926, p. 148 (Cradle Mt., 3000 ft.).

1281.† Coesyra thalamepola Meyr., ibid., 1884, p. 1081 (Sydney, Katoomba).

1282. Coesyra pyrrhoptera Meyr., ibid., 1884, p. 780 (Sydney).

1283. Coesyra rhythmosema, n. sp. (*ῥυθμοσημος*, symmetrical.)

♂. 20–22 mm. Head pale yellow. Palpi with terminal joint three-fifths; pale yellow, basal two-thirds of second joint fuscous. Antennae fuscous; ciliations in male one and a quarter. Thorax dark fuscous; apices of tegulae and a posterior spot pale yellow. Abdomen dark fuscous; tuft ochreous. Legs fuscous. Forewings elongate, slightly dilated, costa gently arched, apex acute, termen sinuate, oblique; pale yellow, markings fuscous; a costal streak from base to three-fourths; a rather narrow oblique fascia from four-fifths costa gradually broadening to dorsum, on which it extends from two-thirds to tornus; a narrow terminal fascia; cilia fuscous. Hindwings and cilia fuscous.

Western Australia: Mogumber in October; two specimens.

1284. Coesyra iotrigona, n. sp. (*ἰοτριγωνος*, with violet triangle.)

♀. 18 mm. Head whitish. Palpi with terminal joint two-thirds; whitish. Antennae pale grey. Thorax pale grey, violet-tinged. Abdomen fuscous; basal segment, apices of segments, and tuft whitish. Legs whitish. Forewings with costa slightly arched, apex round-pointed, termen oblique; yellow; costal edge and dorsum near base violet-tinged;

a large fuscous-edged violet triangle on dorsum from two-thirds to tornus, its apex reaching middle of disc; a narrow terminal fascia violet sprinkled with fuscous; cilia yellow, on apex and tornus grey. Hindwings pale grey; cilia grey-whitish.

Queensland: Toowoomba in October; one specimen received from Mr. W. B. Barnard.

1285. Coesyra iotypa, n. sp. (*ἰοτυπος*, violet-marked.)

♂. 19 mm. Head and thorax yellow. Palpi with terminal joint one-half; yellow. Antennae grey; ciliations in male 2. Abdomen fuscous. Legs whitish-ochreous; anterior pair fuscous. Forewings dilated posteriorly, costa straight, apex acute, termen sinuate, strongly oblique; yellow; a slightly waved fuscous line from three-fifths costa to three-fifths dorsum, and another from three-fifths costa to tornus, area between these violet; costa beyond this and termen suffused with fuscous; cilia yellow, on apex and tornus fuscous. Hindwings and cilia grey.

Queensland: Toowoomba in November; one specimen received from Mr. W. B. Barnard.

1286. Coesyra stenomorpha, n. sp. (*στενομορφος*, narrow.)

♂. 14 mm. Head yellow. Palpi with terminal joint three-fifths; whitish-ochreous, outer surface of second joint except apex fuscous. Antennae fuscous; ciliations in male one and a half. Thorax with anterior half dark fuscous, posterior half yellow. Abdomen fuscous. Legs fuscous; posterior pair grey-whitish. Forewings narrow, costa straight to near apex, apex round-pointed, termen oblique; yellow with fuscous markings; costal edge fuscous; a broad fascia, its anterior edge from two-fifths costa to mid-dorsum, posterior edge irregular from four-fifths costa to tornus, its centre partly suffused with yellow; a narrow terminal fascia broader on costa; cilia fuscous. Hindwings and cilia fuscous.

Victoria: Beaconsfield in January (Dr. W. E. Drake) one specimen; type in Coll. Lyell.

1287. Coesyra triptycha Meyr., P.L.S.N.S.W., 1884, p. 771 (Injune, Milmerran, Brisbane to Melbourne).

1288. Coesyra lactipalpis Meyr., *Exot. Micro.*, ii, p. 382 (Duaringa).

1289. Coesyra cyclotoma Meyr., P.L.S.N.S.W., 1884, p. 771 (Yeppoon to Melbourne, Talwood).

1290. Coesyra acrotropa Meyr., ibid., 1884, p. 779 (Sydney).

1291. Coesyra dichroella Zel., *Hor. Soc. Ross.*, 1877, p. 389; Meyr., ibid., 1884, p. 767; *Gen. Ins.*, Oecoph., Pl. iii, f. 60 = *divisella* Wlk., xxix, p. 685 (praeocc.) = *porphyryplaca* Low., *Tr.R.S.S.Aust.*, 1893, p. 181 (Cape York to Launceston and Adelaide).

1292. Coesyra disticta Turn., *Tr.R.S.S.Aust.*, 1917, p. 72 (Darwin, Cairns to Gympie).

1293. Coesyra cingulata Meyr., ibid., 1884, p. 1045 (Duaringa to Victoria, Mt. Lofty, and Western Australia).

1294.† Coesyra heterozona Low., *Tr.R.S.S.Aust.*, 1894, p. 100 (Duaringa).

1295. Coesyra stereosema Meyr., ibid., 1888, p. 1655 (Tweed Hds., Scone, Bathurst).

1296.† Coesyra anacampta Meyr., *Exot. Micro.*, i, p. 118 (Darwin).

1297. Coesyra ecliptica Meyr., ibid., 1884, p. 775 (Gympie to Victoria).

1298. Coesyra heliciotis, n. sp. (*ἡλικιωτις*, a comrade.)

♂. 14 mm. Head pale yellow. Palpi with terminal joint three-fifths; whitish-ochreous, outer surface of second joint fuscous towards base. Antennae fuscous; ciliations in male one and a half. Thorax fuscous; collar pale yellow. Abdomen grey. Legs fuscous; posterior pair grey. Forewings narrow, somewhat dilated, costa rather strongly arched, termen oblique; pale yellow; markings fuscous; a broad costal streak from base to middle attenuating posteriorly; stigmata minute, first discal at one-third, plical beneath it, second discal before two-thirds; a line from three-fourths costa to tornus, angled inwards on second discal; a narrow terminal fascia; cilia pale yellow, on tornus fuscous. Hindwings and cilia grey. Very like *C. ecliptica*, but differs in the fuscous thorax and the costal streak and stigmata on forewings.

North Queensland: Herberton in July; one specimen.

1299. Coesyra phaeocosma Meyr., ibid., 1888, p. 1655 (Gosford, Fernshaw).

1300. Coesyra sodalis, n. sp. (*sodalis*, companionable.)

♂. 14 mm. Head and thorax pale yellow. Palpi with terminal joint 1; fuscous. (Antennae broken off.) Abdomen grey; tuft whitish-ochreous. Legs fuscous; posterior pair ochreous-whitish. Forewings slightly dilated, costa slightly arched, apex rounded, termen obliquely rounded; pale yellow; a narrow fuscous costal streak to two-fifths; a slightly curved fascia from three-fourths costa to tornus brownish, extremities and anterior edge fuscous; cilia pale yellow, on tornus fuscous. Hindwings and cilia pale grey.

New South Wales: Brunswick Hds. in December; one specimen received from Mr. W. B. Barnard.

1301. Coesyra phaeozona Meyr., ibid., 1888, p. 1656 (Sydney).

1302. Coesyra philoxena Meyr., ibid., 1884, p. 779 (Sydney).

1303. Coesyra delicia Turn., *Tr.R.S.S.Aust.*, 1917, p. 70 (Mt. Tamborine).

1304. Coesyra silacea Turn., ibid., 1917, p. 73 (Brisbane, Milmerran, Stanthorpe).

1305. Coesyra leucanepsia, n. sp. (λευκανεψιος, a white cousin.)

♀. 16 mm. Head white. Palpi with terminal joint three-fourths; white, base of second joint fuscous. Antennae grey. Thorax fuscous. Abdomen whitish-grey. Legs whitish; anterior pair fuscous. Forewings with costa gently arched, apex rounded, termen obliquely rounded; white; a narrow fuscous fascia from three-fourths costa to tornus; cilia white, on tornus grey. Hindwings and cilia grey.

Western Australia: Kalamunda near Perth in December; one specimen received from Mr. W. B. Barnard.

1306. Coesyra parvula Meyr., P.L.S.N.S.W., 1884, p. 783 (Caloundra and Stanthorpe to Tasmania and Mt. Lofty).

1307. Coesyra euerata, n. sp. (εὐηρατος, lovely.)

♂. 14 mm. Head yellow. Palpi with terminal joint two-thirds; whitish-ochreous, base of second joint fuscous. Antennae fuscous; ciliations in male 1. Thorax dark fuscous. Abdomen fuscous. Legs fuscous with whitish-ochreous rings; posterior pair mostly whitish-ochreous. Forewings somewhat dilated, costa slightly arched, apex rounded, termen oblique; yellow; markings purple-fuscous; a basal fascia prolonged on costa to two-fifths; an apical blotch, its anterior edge from five-sixths costa to two-thirds dorsum; cilia fuscous, apices whitish-ochreous except at tornus. Hindwings and cilia grey.

Queensland: Injune in February and March; two specimens received from Mr. W. B. Barnard, who has the type.

1308. Coesyra acnissa, n. sp. (ἀκνισσος, slender.)

♀. 15 mm. Head pale yellow. Palpi with terminal joint three-fifths; brownish. Thorax brownish-fuscous. Abdomen grey. Legs fuscous; posterior pair whitish-ochreous. Forewings with costa gently arched, apex round-pointed, termen obliquely rounded; pale yellow; a moderate brownish-fuscous terminal fascia; cilia brownish-fuscous. Hindwings and cilia pale grey.

Queensland: Adavale in April; two specimens.

1309. Coesyra sidonia Meyr., *Exot. Micro.*, i, p. 119 (Townsville).

1310. Coesyra leptadelpha Low., *Tr.R.S.S.Aust.*, 1920, p. 64 (Cairns).

1311. Coesyra actinodes, n. sp. (ἀκτινωδης, shining.)

♂. 20 mm. Head yellow. Palpi with terminal joint one-half; whitish-ochreous, terminal joint fuscous. Antennae blackish; ciliations in male 5. Thorax and abdomen blackish. Legs blackish; anterior coxae, hairs on posterior tibiae, and tarsal rings ochreous-whitish. Forewings elongate, costa nearly straight, apex pointed, termen very obliquely rounded; yellow; a narrow basal fuscous fascia prolonged on costa to one-fourth; terminal half of wing dark fuscous mottled with shining violet, edged by a curved line from three-fifths costa to mid-dorsum; cilia dark fuscous. Hindwings and cilia dark fuscous.

New South Wales: Maryland near Stanthorpe, Q., in December; one specimen received from Mr. W. B. Barnard.

1312. Coesyra periculosa Meyr., *Exot. Micro.*, i, 120 (Stanthorpe, Sydney).

1313. Coesyra heliophanes Low., *Tr.R.S.S.Aust.*, 1894, p. 100 = *habropis* Low., P.L.S.N.S.W., 1897, p. 20 (Rockhampton, Duaringa, Stanthorpe, Murrurundi).

1314.† Coesyra opsiphanes Low., *Tr.R.S.S.Aust.*, 1894, p. 100 (Duaringa).

THE OSTEOGENESIS OF THE BASE OF THE SAURIAN CRANIUM AND A SEARCH FOR THE PARASPHENOID BONE.

By H. Leighton Kesteven, D.Sc., M.D.

(Forty Text-figures.)

[Read 25th September, 1940.]

Apparently the first description of a parasphenoid bone on the base of the embryonic skull of a reptile was that of Gaupp in his description of the development of the bony skull of *Lacerta* in Hertwig's "Handbuch" in 1906. Since that date various observers have recorded the presence of the bone on the base of other embryonic lacertilian skulls and on the base of embryonic chelonian and crocodilian skulls.

In every instance the bone in question was said to have a very brief independent existence; very rapidly it fused with the basisphenoid bone.

De Beer tells us that in the process of this fusion with the basisphenoid, the parabasal canal—for the ramus palatinus facialis and the palatine terminal branch of the internal carotid artery—is formed between the bones.

In the birds, W. K. Parker described basitemporal bones on the base of the embryonic skull. These were said to fuse later with the basisphenoid and basioccipital bones. These also have, of later years, been identified as parasphenoidal ossifications and have been described as supplying the floor of the parabasal canal, at least in its posterior portion.

This parasphenoid bone of the sauropsidan embryonic skull differs markedly from that of the fishes and amphibians. Though obvious, the points of difference may be itemized here with advantage: (1) The bone fuses early and completely with the basisphenoid; (2) in the result, its independent individuality is a very brief one; (3) its appearance in point of time coincides with ossifications in cartilage and is later than all the other membrane bones.

In view of these differences it was not possible to regard the identification of this tiny squame of bone as the parasphenoid without suspicion. With a view to investigating the question, material for the study of the ossification of the parasphenoid bone in fishes, amphibians, reptiles, and birds, has been collected during the last ten years and the results of the examination of that material are presented here.

It may be stated at the outset that in only one instance amongst the many sauropsidans studied was a bone which might be regarded as a membrane bone found below the cartilaginous basis cranii. This, as will be seen later, was in the early *Varanus* embryo.

Complete series of developmental stages in which one might study the whole process of ossification of the cranium were only obtained in a few instances, but as these included examples of amphibian, lacertilian, chelonian, and avian development, they provided comparative material which enabled one to interpret the pertinent examples amongst the collection of incomplete series and isolated stages of development of reptiles and birds which have come to hand during these years.

i. *Fishes and Amphibians.*

These were studied with the object of observing the relation of the ossifying parasphenoid bone to the superjacent cartilaginous basis cranii, and, as the identity of the bone is in no way in doubt, little need be said. Thanks to the kindly assistance of numerous colleagues, whom I have thanked elsewhere for their cooperation, it has been possible to study an extensive range of Urodeles and Caecillians, as well as two very complete anuran series and several isolated stages of other anuran forms. Amongst

the fishes, material has been available for the study of the development of the parasphenoid in a range of modern acanthopterygian crania, and I have also had for study two stages in the development of *Polypterus*, for which I have to thank Professor Graham Kerr.

Throughout the whole of these lower vertebrata the parasphenoid bone was found to ossify at the same time as the rest of the membrane bones. In every instance a very definite perichondral membrane and, in many instances, connective tissue intervened between the cartilage of the basis cranii and the developing parasphenoid bone. In every instance in which a variety of developmental stages permitted one to make the observation, it was observed that the development of the parasphenoid bone had progressed far before there was any change indicating ossification of the cartilage of the basis cranii. Only in the caecillians was fusion of the parasphenoid bone with a basicranial cartilage bone observed. In several of these the parachordal cartilages were seen unchanged and enclosed by their perichondral membrane, with the parasphenoid well developed and extending laterally beyond the cartilages. These parachordal rods continued backward to join the narrow occipital basicranial bar which, itself, was in process of ossification. Fusion between this occipital ossification and the hinder end of the parasphenoid was observed in later stages of development. It is believed that the basisphenoidal region of the base of the skull in the caecillians is ossified only by the parasphenoid. This same condition is also observed in some urodele skulls, but in these the cartilaginous basis cranii is more extensive and persists in adult stages. Fusion between the parasphenoid and the overlying endochondral basicranial and otocranial elements is to be seen in some anuran skulls, but the fusion takes place some time after the metamorphosis has been completed, and is to be compared with the closure of the sutures which takes place between so many of the bones in the skulls of higher vertebrates.

ii. *Reptiles.*

A. Lacertilia.

1. *Physignathus lesueurii* (Figs. 1–8).

The eggs of this agamid lizard take one hundred and eleven to one hundred and seventeen days to hatch out. I have been fortunate in obtaining several hundred of the eggs at all stages of incubation, and have been able to study the whole process of ossification of the skull. The head length changes very slightly during the last five weeks of development. At the beginning of this last five weeks the complete chondrocranium shows no sign of ossific changes, but several of the membrane bones have commenced ossifying. Two weeks later all the membrane bones are well established and early ossific changes are apparent in the cartilage of the basis cranii and in the upper anterior portion of the otocrane. There is no bony formation whatsoever below the cranial base in the basisphenoidal or occipital regions. The ossification of the chondrocranium is not completed until three to four weeks after the young hatch out.

The great majority of the eggs were laid during the last week of October and the first week of November, and as twelve to fifteen were laid in the one hole at the one time they were always collected in batches. This made it possible to date every specimen preserved with a high degree of accuracy, by the simple procedure of always leaving the last specimen in every batch to hatch out. Each batch, as collected, was dated provisionally as having been laid on November first, with a probable margin of error of seven days; they were then allowed to hatch for the period required to fill a gap in the series obtained at the time of their collection; all but one would then be preserved on successive days; when the last hatched out, one corrected the error in their estimated age. The numbering of my stages is an indication, with a fair degree of accuracy, of the period of hatching. One hundred and fourteen days have been taken as the full period of incubation.

Magnified images of the sections were obtained with a vertical projector made for me by Messrs. E. Esdaile and Sons of Sydney. All the drawings have been made by tracing these projected images.

Ossification of the membrane bones commences about the seventy-fifth day and by the eighty-fifth all are well established. This eighty-fifth stage is of particular interest. The chondrocranium has reached its full development and shows no ossific changes anywhere. The internal cerebral branch of the internal carotid artery is seen here as it passes mediad, rostrad and dorsad to reach the pituitary fossa, lying embedded in a groove on the cartilaginous basis cranii. This groove is open antero-inferiorly (Figs. 1 and 2).*

Particular interest attaches to the situation of this artery at this stage, because the relation of the vessel to the basis cranii in earlier stages might very easily lead to erroneous interpretations, had one not been able to study this stage. From the thirty-fifth day, and perhaps somewhat earlier, the chondrocranium has developed all its parts, and from then on undergoes little change. Thereafter, however, the basis cranii gradually undergoes considerable dorsi-ventral thickening, and this reaches its maximum by the eighty-fifth day. Before this thickening takes place the cerebral artery reaches the pituitary fossa without being in contact with the cartilage at all. Figure 3 is taken from a specimen at stage thirty-five, and represents the same region as the illustrations of stage eighty-five. The cranial basal cartilage is actually thinner than the drawing would lead one to believe because the section is slightly inclined to the transverse vertical plane. The head length of stage eighty-five was 10 mm.

In stage ninety, head length 10·8 mm., the only change of note is that the flange of cartilage which stands down and slightly forward behind the cerebral artery has undergone early ossific change.

In stage ninety-two, with a head length of 11·0 mm., spicules of bone are visible in this flange; and the upper surface of the strong membrane which closes the pituitary fossa below has become invaded by osteogenetic tissue. This tissue is continuous with that present along the edge of the cartilage behind the artery.

Apparently it is this ectochondral ossification of the basisphenoidal cartilage which has been identified as the postero-lateral wings of the parasphenoid.

In stage one hundred and five, with a head length of 12·0 mm., the median piece of bone which has been regarded by authors as parasphenoidal is present above the subpituitary membrane, forming a complete bony bar across the floor of the fossa (Fig. 4). In the next section behind this, however, this bone is found to be in complete continuity with lamellae which almost completely surround the trabecular cartilages and which are, beyond doubt, ectochondral ossifications of the cartilage which, itself, may be seen undergoing early ossific changes on each side (Fig. 5). In the section next behind this the whole of both cartilages are found to have broken down and to be entirely surrounded by bony lamellae of ectochondral origin; furthermore, there is intramembranous extension from this latter bone dorso-laterally, most extensive on the left side (Fig. 6). In the next section the union of the pericartilaginous bone lamella of the left side with the ventral table of the basipterygoid ossification is found (Fig. 7). The palatine artery and ramus palatinus facialis, lying on the upper surface of the last lamella, are clearly not resting on a parasphenoidal ossification. Behind the division of the vessel, the internal carotid artery and the ramus palatinus facialis are

* The lettering on the Text-figures is as follows: *A.c.e.*, arteria corotis externa; *A.c.i.*, arteria corotis interna; *Ang.*, angular bone; *Ant.s.can.*, anterior semicircular canal; *Art.c.* and *Art.cer.*, arteria cerebralis; *Art.pal.*, arteria palatina; *Art. vert.*, arteria vertebralis; *B.sph.* and *Ba.sph.*, basisphenoid bone; *Can.p.b.*, canalis parabasalis; *Dent.*, dentary bone; *D.m.*, dura mater; *Epi.pt.*, ascending process of the quadrate; *Eust.r.*, eustachian canal; *Men.pt.*, meniscus pterygoideus; *Mk.*, Meckel's cartilage; *M.pg.*, pterygoid muscle; *M.rect.ext.* and *Mus.rect.ext.*, external rectus muscle; *N.ph.*, eustachian aditus; *O.c.b.*, original boundary of the cartilage; *Opt.ch.*, optic chiasma; *Os.pal.*, palatine bone; *Os.pg.*, pterygoid bone; *P.ant.* and *Pila ant.*, pila antotica; *P.ch.*, proliferating perichondrium; *P.c.o.*, perichondrium cut obliquely; *Ph.*, pharynx; *Pit.*, pituitary body; *Pit.ant.*, pituitary body, anterior lobe; *Pit.post.*, pituitary body, posterior lobe; *Pit.v.*, pituitary vein; *P.sph.* and *Pr.sph.*, presphenoid ossification; *Pr.b.pt.*, processus basipterygoideus; *Pro.ot.*, prootic cartilage or bone; *Pr.pal.pt.*, palato-pterygoid process; *Pt.str.*, subpituitary membrane; *Qu.*, quadrate; *R.sph.* and *Ros.sph.*, Rostrum basisphenoidei; *T.m.*, Taenia marginata; *Trab.*, trabecula; *Tr.cr.*, trabecular crest; *Ty.*, tympanic cavity; *Ven.*, a vein or a venous sinus; *Vena c.l.*, vena capitis lateralis; *Ven.orb.* vena orbitalis; *Ven.sin.*, a venous sinus.

found lying in a canal which is definitely surrounded entirely by basisphenoid bone (Fig. 8). Where these two structures enter that canal posteriorly they lie in a groove on the side of the basisphenoid with only the ventral table of that bone below them.

There are two aspects of the findings in these embryos which lead one to feel confident that no parasphenoid bone is developed. Firstly, the appearances certainly justify the belief that the only squames which might be identified as parasphenoidal are in reality only intramembranous extension of ectochondral ossifications, basisphenoidal in origin. If, one the other hand, we were to regard these intramembranous extensions as entirely membranous in origin, it would be difficult to understand their extremely brief independent existence. In estimating the age of the stages, a possible error of four days is admitted. Assuming that my stage ninety-two would have taken one hundred and seventeen days to hatch out, then it should have been numbered

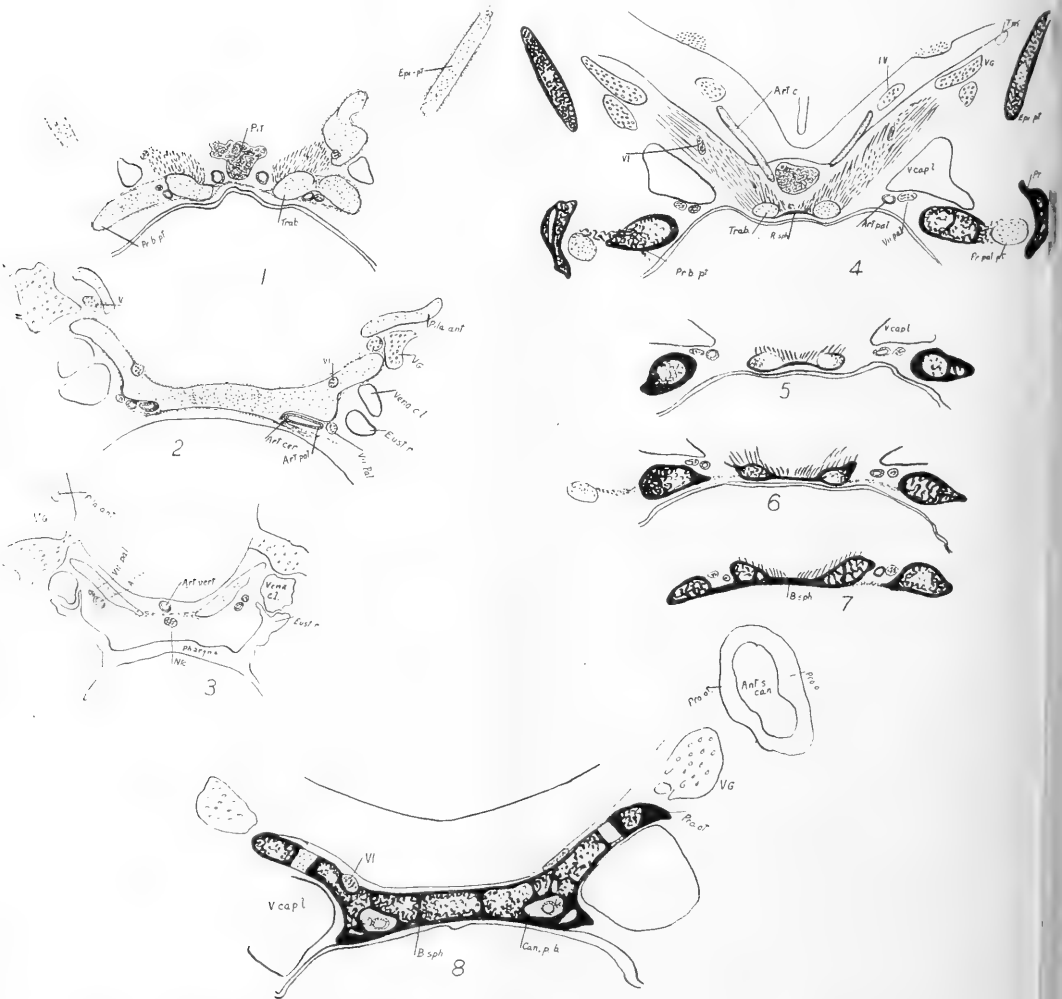


Fig. 1.—*Physignathus*. Stage 85. Transverse section through the pituitary fontanelle just behind the root of the basipterygoid process.

Fig. 2.—Another section through the same specimen, just in front of the junction of the pila antotica to the trabecular crest.

Fig. 3.—*Physignathus*. Stage 35. This section is from approximately the same location as that illustrated in Fig. 2.

Figs. 4-8.—*Physignathus*. Stage 105. Transverse sections through the pituitary and post-pituitary region.

eighty-nine; if, on the other hand, it would have taken only one hundred and eleven days it should have been numbered ninety-six.

Now, it is possible that the fusion of the intramembranous squames took place a day or two earlier than stage one hundred and five, but even if it be assumed that the fusion took place on that day, it still remains the fact that these squames could have had an independent existence for a maximum of fifteen days, while the probability is that the period was less than ten.

In view of all the facts, it is concluded that these squames are intramembranous extensions of basisphenoidal ossification. This conclusion is further supported by the fact that they differ in no way from the intramembranous extensions of that bone in the anterior portion of the basicranial vacuity and antero-dorsally between the basis cranii and the prootic ossification, nor do they differ from the intramembranous extension of the basioccipital ossification across the basicranial vacuity in its posterior portion.

2. *Diporophorus* sp. (Figs. 9, 10, 11).

For the opportunity of studying this agamid lizard I am indebted to Mr. Kinghorn, through whom I obtained three specimens of the one, late, stage of development, and who, himself, presented me with one slightly earlier embryo.

I illustrate three successive sections through the pituitary region of the elder of the two stages.

The first of these is of interest as showing a tiny squame beneath the pituitary fossa which, taken alone, might be mistaken for a parasphenoidal ossification. Actually this spicule of bone is present in two sections in front of that drawn, but in the section next illustrated (Fig. 10) the continuity of the spicule with the basisphenoid bone is demonstrated. This is not due to the fusion of a membrane bone with the base of the basisphenoid, for there is no trace of the spicule in the same location in the younger stage, in which the trabeculae are unchanged cartilage in, as nearly as may be judged, the same location as the second of the three sections here drawn (compare Fig. 12). In this earlier stage there is no medially projecting extension of the basisphenoidal ossification till some three or four sections further back, and then there is complete continuity from side to side, as in the third section figured here.

These facts lead me to assert with a fair degree of confidence that the median spicule is simply an extension in membrane of the basisphenoidal ossification.

3. *Tiliqua scincoides* (Figs. 12–16).

Two specimens of interest are available for study. Both are late stages, comparable in point of development with the stages 105 and 114 of *Physignathus* just described. For the younger I have to thank Mr. Kinghorn and the Trustees of the Australian Museum, for the other I am indebted to my son Geoffrey L. Kesteven.

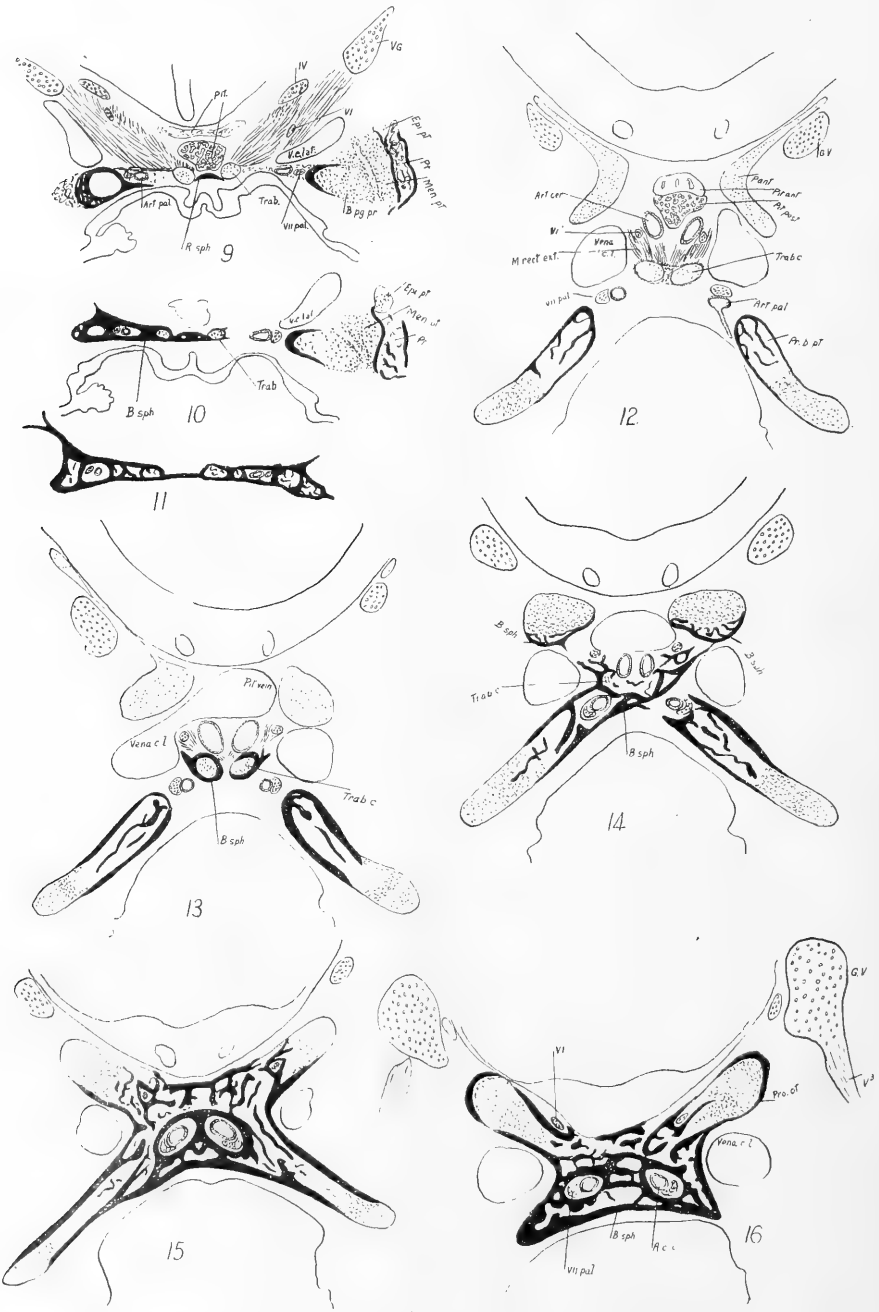
Particular interest attaches to these two scincoid specimens in that the younger corresponds also in point of development with the *Lygosoma* embryo studied by Pearson (1921). Pearson described the ossifications present in her specimen and did not mention the presence of a parasphenoid. It would appear, in the light of the findings in my scincoid embryos, that this was not an oversight, but was because there was no evidence of the presence of the bone in the *Lygosoma*.*

Stage A so closely resembles the later stage that it does not call for separate description. It shows no trace of any membrane bone beneath the basis cranii. At Stage B all the membrane bones are well advanced in ossification and have assumed the adult relations and proportions.

Figure 12 is taken from section No. 167 and is two sections behind the separation of the trabecula communis into its component cartilages. The two trabecular rods are seen side by side and separated by the perichondrium of the junction. It will be observed that there is no spicule of bone beneath the cartilages. The processus basipterygoideus is cut where it projects down and forward in front of its junction with the body of the basisphenoid. The proximal end of the process is completely ossified, the distal end unchanged cartilage; the intervening length is vacuolated

* See the description of *Lygosoma* later.

cartilage in process of ossification. The pila antotica and anterolateral corner of the basisphenoid cartilage are seen on either side of the pituitary gland and extending dorsolaterally thereto. The posterior end of the external rectus muscle attached to the perichondrium of the trabeculae lies beneath the two internal cerebral arteries and the pituitary gland, the abducent nerve lies amongst the muscle fibres beside the artery.



Figs. 9-11.—*Diphorophorus.* Stage B. Transverse sections through the pituitary region.

Figs. 12-16.—*Tiliqua.* Stage B. Transverse sections through the pituitary and post-pituitary region.

The resemblance of these last features to those described for *Lygosoma* by Pearson will be noted. The internal carotid artery has, of course, been cut in front of its division; the palatine branch, accompanied by the ramus palatinus facialis is situated, as will be seen from later sections, in front of the middle of the height of the junction of the basipterygoid process and the body of the basisphenoid. The vena capitis lateralis is placed immediately above the last two mentioned structures.

Figure 13 is taken from the next section but one, No. 169. Here one need only remark upon the fact that both the cartilaginous rods are completely surrounded by bone and that the cartilages themselves are undergoing ossific changes.

In the next section, No. 170 (Fig. 14), the complete continuity of the bone, developed ectochondrally, around the posterior end of the cartilage with the upper and lower bony tables of the basisphenoid bone is very evident on the left side. It is equally evident here that the parabasal canal lies enclosed only by the basiphenoid bone.

The two illustrations (Figs. 15, 16) from sections 173 and 175, are produced to show quite conclusively that the parabasal canal lies entirely within the basisphenoid bone. These sections provide definite evidence that no parasphenoidal ossification is present on the base of the skull.

4. *Varanus* (Figs. 17–21).

Stage A.—Unfortunately my two embryos of this lizard cannot be usefully described by a reference to the head length because the younger is specifically unidentifiable. The stage of development of this embryo is closely comparable with stage 85 in the *Physignathus* series. The membrane bones are all well established, whilst endochondral

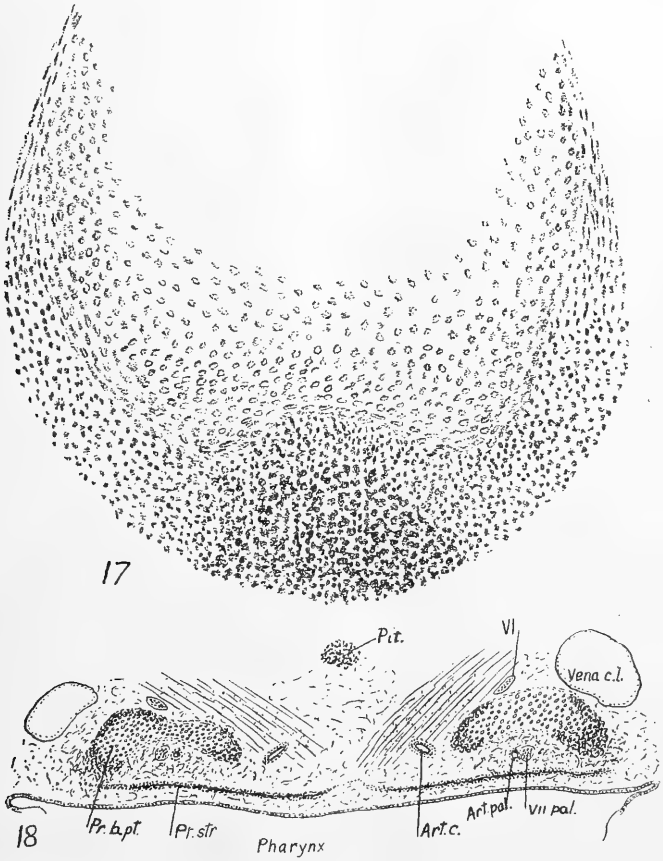


Fig. 17.—*Varanus.* Stage A. A transverse section through the ventral portion of the posterior end of the intorbital septum.

Fig. 18.—*Varanus.* Stage A. A transverse section through the pituitary region.

ossification is just at its inception, as evidenced by degeneration of the cartilage cells in some places.

Figure 17 illustrates the early changes in the perichondrium on the lower surface of the intorbital septum a short distance in front of the pituitary fontanelle. This early change takes the form of a proliferation of the deep layer of the perichondrium and a breakdown of the membranous outer layer, so that there is no defined boundary between the osteogenetic and the contiguous connective tissues. The process closely resembles that seen in the birds, but the extent of the invasion of the connective tissue is far less. Since the process commences at, or near, the hinder end of the intorbital septum and extends forward as development progresses, a very similar picture is presented at the fore end of the septum in the later stage. The illustration has been drawn from the earlier stage because the wider base in this location offers a bigger field to illustrate.

Figure 18 is taken from the same series of sections as Figure 17; it is through the pituitary region, in front of the arterial canal and just at the root of the basipterygoid process. Here we see the only structure which I was inclined to regard as a parasphenoid bone in the whole of my collection of saurian embryos. It is a thin sheet of densely packed, deeply staining cells which lies beneath the pituitary fontanelle, and which, at its lateral edges, contains tiny spicules of bone (pt.str.). As seen in its entirety from below, this sheet would have the general outline of two right-angled triangles, with their lateral sides about one-half the length of the anterior side, joined at the antero-medial corner and with the postero-lateral corners produced into a short parallel-sided spur. The anterior, sinuated, nearly transverse margin of this sheet of cells lies free with connective tissues both above and below it, and is situated below the hinder end of the pituitary fontanelle. The lateral and the postero-medial margins blend imperceptibly and completely with the perichondrium of the basis cranii.

This sheet is, then, proliferated from the basal perichondrium, and it is only the very wide character of the fontanelle which makes this look different from the conditions found in all the other lacertilian embryos examined.

It may be recorded that the early closure of the basicranial fontanelle is effected in this lizard in precisely the same manner as the pituitary fontanelle, that is to say, by a delicate bony squame developed in cellular tissue which is continuous with the perichondrium and is therefore presumed to have been proliferated from the deep layer of that membrane.

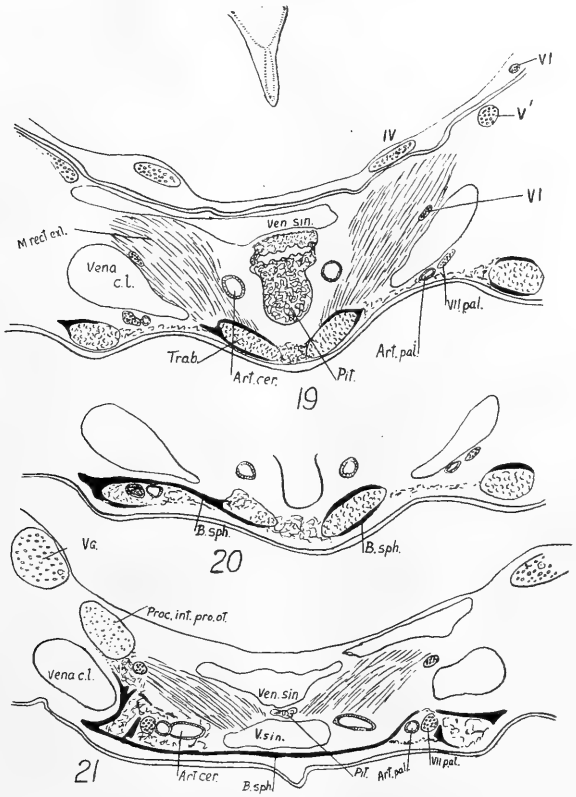
It follows, then, that both of these squames are membrane bones, or that neither of them is.

Stage B.—I have to thank Mr. Kinghorn for four late embryos of *Varanus varius*. These were obtained from a rabbit burrow, and were due to have hatched out in another week or two in all probability. They are very probably about three to four weeks older than the earlier embryos, as judged by comparison with the rate of bone development in *Physignathus*. They are a little further advanced than stage 105 of that species, but not so far as 114.

All the membrane bones are well established and ossification of the chondrocranium is well under way.

There is no trace of any bony lamella or spicule beneath the trabecula communis or anterior end of the pituitary fontanelle (Fig. 19). In the transverse section illustrated, No. 145 of my series C, it will be seen that, though the trabecular cartilages are in process of breaking down prior to ossification, there is no lamella beneath the pituitary vacuity. The dorsolateral ends of both the cartilages are surrounded by ectochondral bone, and this on the left side shows a linear intramembranous extension towards the distal end of the processus basipterygoideus. In the next section, No. 146 (Fig. 20), the continuity of this linear extension with the upper lamella of the basipterygoid ossification proves conclusively that it cannot be regarded as a parasphenoidal ossification, although it is very definitely related to the under surface of the trabecular cartilage. Since there is no bony lamella beneath it, it would appear certain that there cannot be any parasphenoid bone present.

In section No. 149 (Fig. 21) a lamella is found connecting the chondral ossifications of each side. This has the appearance of the parasphenoid on the base of the caecillian skull, but there is little room for doubt that it is in reality an intramembranous extension of basisphenoidal ossification. It is similar in all respects to the lamella which, further forward, connects the upper surface of the ossification of the basipterygoid process to the under surface of the trabecular ectochondral ossification.



Figs. 19-21.—*Varanus.* Stage B. Transverse sections through the pituitary region.

5. *Lygosoma* (*Hinulia*) *guichenotii* (Fig. 22).

The eggs of this common little "Black Fence Lizard" are laid from early in November till the middle of December, and hatch out in about sixty days.

My very complete series of embryos of the species enables me to record that Pearson's (1921) failure to mention the parasphenoid bone was not an omission; there is never any trace of the bone. De Beer's interpretation of Pearson's report is, therefore, erroneous in the statement that the palatine nerve emerges from the Vidian canal "dorsally to the parasphenoid" (1937, p. 237).

My illustration is drawn from section 59 of one of my series of stage 50, about ten days before hatching. During the last few days the head length is practically unchanged.

The ossification of both dorsal and ventral surfaces of the basitrabecular cartilages is obvious, and the endochondral ossification is well advanced. The parabasal canal is clearly lodged in the cartilage on the right side; on the left, slightly further forward, the canal has almost reached its anterior opening.

Résumé.

It appears then that, except for a tiny squame of bone of fleeting independence, there is no evidence of any parasphenoid bone on the base of any one of the lacertilian embryos studied. It is believed that the squame of bone mentioned is developed from osteogenetic tissue proliferated from the deep layer of the perichondrium of the cranium.

It may be remarked, in conclusion, that the origin of the rectus externus muscle from the floor and side wall of the pituitary fossa, first recorded by Pearson (1921), is not peculiar to *Lygosoma*, but is present in every one of these lacertilian embryos.

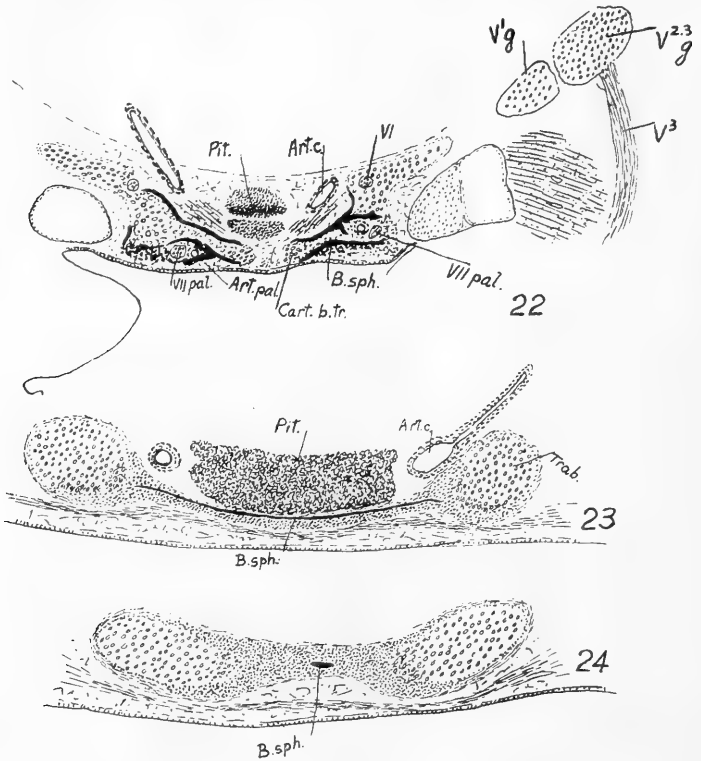


Fig. 22.—*Lygosoma* (*Hinulia*). A transverse section through the pituitary region.
Figs. 23, 24.—*Chelodina*. Stage A. A transverse section through the pituitary region.

B. Chelonia.

1. *Chelodina longicollis* (Figs. 23, 24, 25).

This "River Turtle" is fairly common in the rivers and lakes of New South Wales, and I have been fortunate in obtaining a number of embryos of different ages. For these my thanks are due to Mr. Stanley Mabury, the Manager of my farm on the Myall River, N.S.W.

My first two illustrations are drawn from transverse sections through the pituitary and prepituitary regions of an embryo with head length of 9·5 mm.

The appearance here is very similar to that observed in the younger embryo of *Varanus*, but, as it was studied after that, the squame of bone below the pituitary fontanelle was not mistaken for a parasphenoid, as was that other when first seen.

This squame of bone lies, very definitely, above a layer of closely-packed cellular tissue, which is continuous with cellular tissue which lies in contact with the medial surface of the trabecular cartilage, and which is covered both superiorly and inferiorly by the outer, membranous layer of the perichondrium (Fig. 23). In a section a little further forward the extreme tip of this bony lamella is seen lying in the midst of a

strand of cellular tissue which extends from one cartilage to the other (Fig. 24). There is little reason to doubt that this bony lamella is a membranous extension from endoperichondral ossification.

Figure 25 is drawn from a section through the head of an embryo with a head length of 9·8 mm. Here, it will be observed, the trabecular cartilages are surrounded by bone, proving quite conclusively that the ossification of the cranium in this region is, at first, endoperichondral. The bone surrounding the cartilages is absolutely continuous with that between the cartilages, and with that which extends dorso-laterally from them. There can be no doubt that we view, here, the basisphenoid bone. It seems, in view of the very complete, and very rapid, fusion of the lamella seen in the younger embryo with the rest of the basisphenoid bone, that it would be wrong to regard the lamella as a parasphenoid bone.

There is no other structure present which could be so identified. There is little doubt, however, that this is the "small plate of bone under the hypophysial fenestra" (de Beer, 1937, p. 259) which has been so identified in other chelonian embryos.

C. Ophidia.

1. Python.

I have but a single stage in the development of this snake. The chondrocranium is fully formed and most of the membrane bones have commenced to ossify.

Ossification of the basisphenoid is definitely endochondral. Small areas of broken-down cartilage and very early bone formation are present on either side of the pituitary fontanelle. No trace of, and nothing which could be mistaken for, a parasphenoidal ossification is visible. The pituitary fontanelle is supplied with a floor of dense membrane as in the other reptiles studied.

It is generally agreed that there is no parasphenoid developed in the ophidian embryonic skull; this is probably because, in the ophidia, the ossification of the basisphenoid is endochondral and therefore the ventral table of the bone is not completed or, indeed, even initiated before the cancellous tissue.

There is no doubt that the general agreement upon the absence of the parasphenoid from the ophidian embryonic skull is correct; there is no such bone here. This fact is to be regarded as evidence that the so-called parasphenoid bone of other reptilian embryonic skulls is in reality only the ventral table of the ectochondrally developed basisphenoid bone, for it is difficult to understand why, if the bone be present in those, it should not be present also in the ophidians.

2 and 3. *Pseudechis* and *Dendrophis*.

These two snake embryos were both taken from the egg just before hatching, and ossification is nearly complete in both of them. The *Pseudechis* is slightly the younger and in it the ventral table of the parasphenoid is complete. The dorsal table shows some areas not yet ossified. No trace of a parasphenoid ossification is to be seen in either skull.

iii. *Aves*.

General statement.

The kindly assistance of several friends has made it possible for me to examine the embryos of sixteen different birds in the present investigation. I have to thank Mr. H. C. Mawhiney of St. George, Queensland, for the series of Emu embryos, I am indebted to the late Dr. J. Allan Thomson, late Director of the Dominion Museum, Wellington, New Zealand, for the *Apteryx*, and all but two of the Australian birds were collected for me by Messrs. H. A. Blakeney and J. S. P. Ramsay, who were good enough to make special excursions for them.

It may be stressed that the process of ossification of the avian basis cranii, as described below, is not peculiar to that part of the chondrocranium, but is similar to the process of ossification of the chondrocranium in all its parts, and is characteristic of, and peculiar to, the aves. It is probably causally related to the pneumatization of the bones.

The earliest observed change leading to ossification takes the form of a cellular proliferation of the perichondrium, and is seen first below the trabecular communis and

the trabeculae on either side of the pituitary fontanelle. This thickening of the perichondrium is particularly marked towards the posterior end of the intorbital septum. At the anterior boundary of the pituitary fossa the area of proliferation splits into two, and each half is continued backwards along the ventro-medial surface of the cartilage on each side of the fontanelle, and then on to reach the basicranial cartilages on each side of the basicranial fontanelle. At the point of divergence of the trabeculae, the area of proliferation not only divides onto the ventra of the two rods, but also extends directly backwards between the diverging rods so that for quite an appreciable distance the areas of proliferation on the ventro-medial surfaces of the cartilages are connected by this proliferation into the tissues below the fontanelle.

Following the cellular proliferation of the deep layer of the perichondrium there is a loss of definition of the outer layer, and this is followed by invasion of the connective tissue in immediate proximity to it by further proliferation of the earlier layer. This later phase, however, leads to the development of an area, rich in cellular elements, but differing from the early stage in that they are not so closely packed and that the cytoplasm of the majority of the cells takes the basic stains more intensely, and the nuclei do not, therefore, stand out so clearly. The process continues by further invasion of the surrounding tissue and by the aggregation of the cells into irregularly disposed masses. Definite osteoblasts next become recognizable, and their appearance is rapidly followed by the formation of bony spicules. These spicules appear first, for the most part, in contact with the surface of the cartilage, but always in the midst of an aggregation of the cells. Meanwhile the superficial cartilage cells have undergone early degenerative changes.

The ossification of the base of the intorbital septum commences near the posterior end and takes several days to reach the anterior end, so that the whole of these changes in the periosteum leading to early ossification may be studied in a single specimen of appropriate age. The fourteen and one-half day chick is a perfectly satisfactory example. I have been able to observe the process in *Apteryx*, Emu, *Phalacrocorax*, *Recurvirostra*, *Podiceps*, *Botaurus*, *Melopsittacus*, *Acrocephalus*, *Himantopus*, *Erythrogonys*, *Iredipara*, *Gallus* and *Anas*.

A detailed description of the histological changes at the various stages in this process of ossification will be given elsewhere; here we are interested in the question of the presence or absence of parasphenoidal ossifications on the avian cranial base, and proceed to selected descriptions of observed conditions which throw light on this particular question.

Since the first bony formation is, throughout the birds, always the ventral edge of the intorbital septum and the ventral table of the basisphenoidal, otocranial and basioccipital regions, there is always formed a bony squame, triangular in outline and with an elongated splint-like rostral projection. This is the structure which has been identified as the parasphenoid bone. Apparently the basisphenoidal wings of this squame may, at times, be separately formed, giving rise to the so-called basitemporals, but none of my many specimens show this feature.

The earliest portions of this "parasphenoid" to be formed are the basiseptal and basisphenoidal, but, quite uninterrupted continued growth carries it back and laterally to underlie the whole of the otocranial and basioccipital regions, as just stated. Therefore, if there be a parasphenoid bone here at all it should be credited with covering the whole of the basis cranii, and not merely part of it; any limitation must be by purely arbitrary definition. As against this view, however, there is the fact that, even before the ventral table has covered the areas said to be protected by a parasphenoid, the earliest formed portion of the squame has been added to by endochondral ossification, so that this so-called parasphenoid has already completely fused with the basisphenoid before it has developed to its full superficial extent. Quite apart from the histological evidence that the whole ventral table is an endo-perichondral ossification, it would surely not be correct to identify as separate entities portions of bone which have so brief an independent existence. In support of this view, it may be pointed out that the rigid observance of such a procedure would involve the necessity

of recognizing as independent ossifications quite a number of primary centres of ossification. For example, in the majority of the birds, if not in all, the basisphenoid bone is ossified from five endo-perichondral centres: one ventral, two on the ventro-medial wall of the lateral arterial canal, and two on the dorso-lateral wall, all essentially similar. If the ventral is a membrane bone, so also are the others, and we must regard the basisphenoid bone as having been formed by the fusion of five membrane bones with the endochondral bone, truly a *reductio ad absurdum*.

There is yet another feature of general occurrence which bears upon the question. Wherever there is an extension of a chondral bone, the extension is preceded by invasion of the area by osteogenetic tissue which is proliferated from that which has

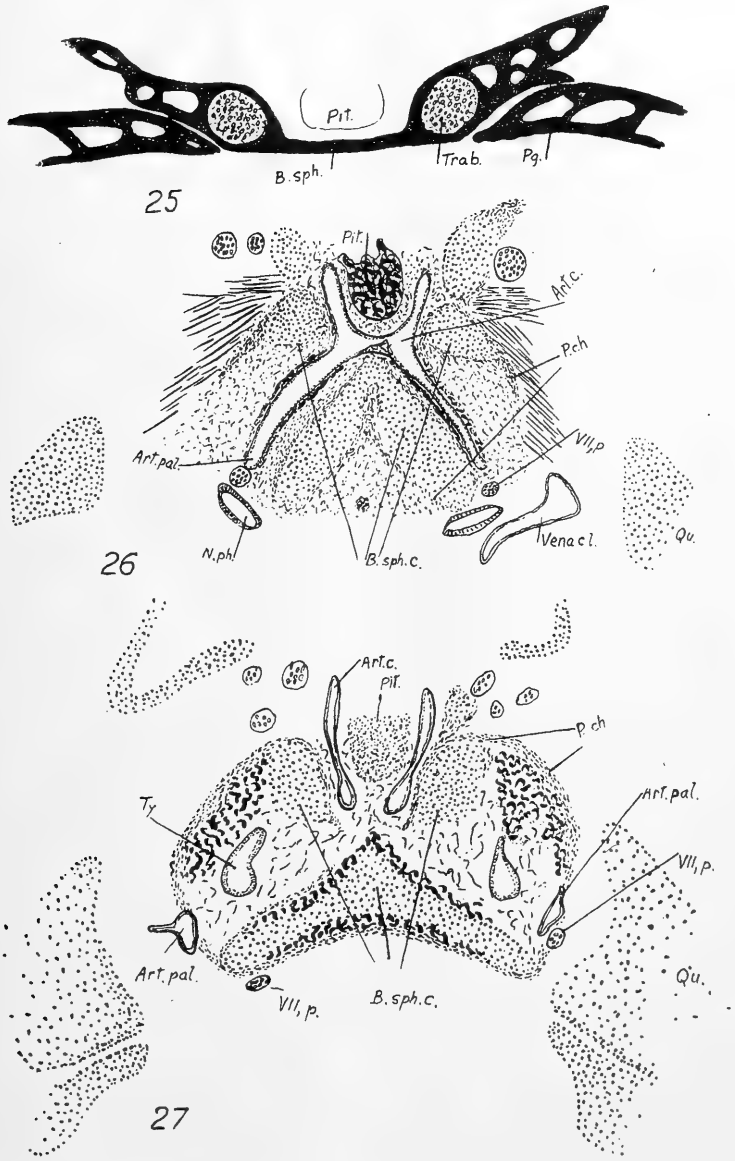


Fig. 25.—*Chelodina*. Stage C. Transverse sections through the pituitary region.
Fig. 26.—Emu, head length 22 mm. A transverse section through the pituitary region.
Fig. 27.—Emu, head length 37 mm. A transverse section from the same location as Fig. 26.

given rise to the bone from which the extension has taken place. This invading osteogenetic tissue is precisely similar to that which gives rise to the bony squames first formed all round the cartilage.

Finally, further support for the interpretation of the ventral bony squame adopted here is found on comparing the formation of the truly membrano-genetic dentary around Meckel's cartilage with these other squames. Throughout the whole growing period there is no trace of any change in the perichondrium and the osteogenetic tissue is always clearly distinct from that membrane.

Detailed descriptions.

1. The Emu, *Dromaius novaehollandiae* Latham* (Figs. 26–29).

Stage A.—Head length 22 mm. The section illustrated (Fig. 26) includes nearly the full length of the internal cerebral arteries and their cross commissure, within the lateral arterial canal, and the pituitary fossa. The position is just behind the pituitary fontanelle, and the section shows the trabeculae just after their union at the back of that vacuity. The anterior tip of the notochord lies a little further back.

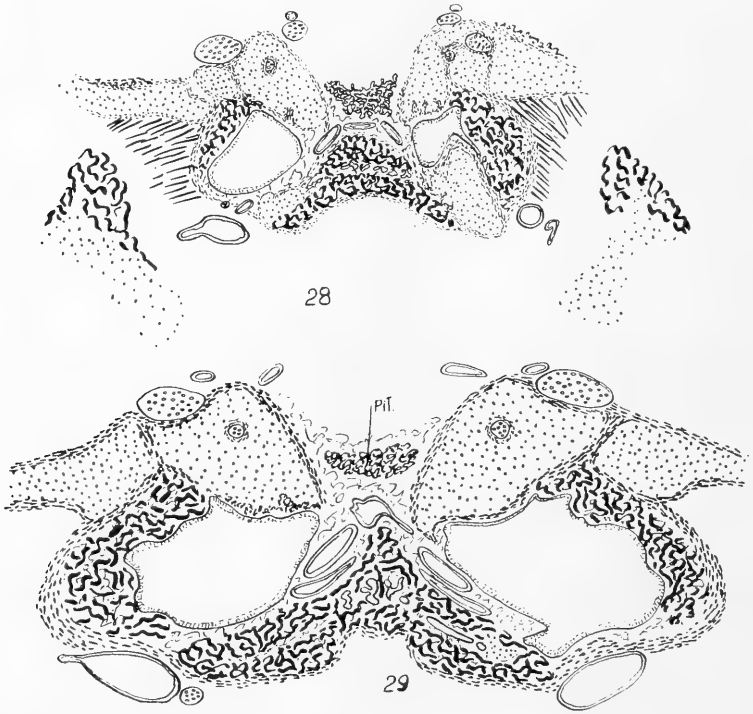


Fig. 28.—Emu, head length 40 mm. A transverse section from the same location as Fig. 26.

Fig. 29.—Emu, head length 45 mm. A transverse section from the same location as Fig. 26.

Interest attaches particularly to the proliferation of the perichondrium at the mid-line and on either side thereof below the cartilages, from the ventro-lateral corner of the cartilage above the canal and along the dorso-lateral surface of the cartilages below the canal (Fig. 26, P. ch.). Particular interest must attach to the second of these areas of proliferation, for it extends a considerable distance from the cartilage. Later stages will show that the greater part of the loose connective tissue between this band of osteogenetic tissue and the artery will be absorbed to make room for the

* The nomenclature of this communication is taken from a popular work, "What Bird is That?" by Neville Cayley (1939).

anterior recess of the tympanic cavity. The absence of proliferation of the perichondrium around the ventro-lateral corner of the cartilages is noteworthy.

Stage B.—Head length 37 mm. (Fig. 27). The length of the cerebral artery included in the section indicates that this is fairly comparable with the preceding section. Particular interest attaches to the areas of early ossification. It will be observed that they are all in precisely the locations in which proliferation of the perichondrium was observed in the earlier stage.*

The five centres of ossification of the basiphenoid, mentioned above, are seen in this section, but the two on the floor of the arterial canal have fused medially. If there be a true membrane bone shown in the section it must surely be that which lies dorso-laterally to the anterior recess of the tympanic cavity, for it alone is formed independently of cartilage. That is, independently if we disregard the fact that its osteogenetic tissue was proliferated from the perichondrium.

The ventral squame is uninterruptedly continuous with the basi-septal "parasphenoid" rostral splint.

Stage C.—Head length 40 mm. (Fig. 28). The presence of a section of the cerebral artery indicates that the section has been cut in close proximity to the situation of the others. Here the dorsal and ventral tables, below the pituitary fossa, have almost fused, whilst as yet the lateral corners of the cartilage are but little changed.

Stage D.—Head length 45 mm. (Fig. 29). The cartilage below the fossa has been almost completely replaced by bone. It will be observed that this replacement has been brought about by the equal extension of *similar* dorsal and ventral areas of ossification, and that long before this stage was reached both dorsal and ventral superficial squames had lost their identity.

2. *Melopsittacus undulatus* Shaw (Figs. 30, 31).

I have to thank Mr. M. Brennan of Earlwood, Sydney, for a very complete and perfectly preserved series of embryos of this little Parrakeet. He obtained them for me from his own aviary, so that the period of hatching is as accurately known as is possible. The two sections illustrated are both taken from the same transverse series of an embryo of the fourteenth day of hatching.

Figure 30 is taken from a section through the intorbital septum towards its posterior end. This section has been selected for illustration because the presence of a venous sinus between the osteogenetic stromata of the presphenoid and pterygoid bones demonstrates very conclusively that these are not continuous. In other locations they are separated by quite a wide interval of connective tissue or, where they appear to be continuous, by a thin membrane. The question which their apparent continuity in some locations raised was: In view of the fact that pterygoid and palatine bones are, in this bird, developed from one continuous osteogenetic stroma, is that from which the presphenoid basal ossification developed part of that same stroma? Careful study of the sections in front of and behind the sinus, where the apparent continuity is seen, shows that the question may be confidently answered in the negative. It may be remarked that the apparent unity of the two stromata was suggested by their close similarity as well as by the apparent continuity. The illustration is further selected to show the proliferation of the perichondrium below the septum and the massing of the osteoblasts within that proliferation.

The continuity of the stromata of the pterygoid and palatine bones is of interest. It has been observed that it is not unusual in the developing bird head to find the osteogenetic stromata of contiguous membrane bones to be quite continuous in the younger embryos. This may be observed particularly around Meckel's cartilage, where the stromata, from which angular, surangular, splenial and dentary bones are developed, are at first quite continuous. It is of particular interest, in this connection, that the osteogenetic stroma of the articularis, on the other hand, always remains quite definitely separated from those of the contiguous membrane bones.

* It may be permissible to stress the fact that all the illustrations have been made by direct tracing of the projected image of the section, using a lantern projector especially devised for the purpose; that these tracings were transferred directly for the final drawing and were not copied freehand.

Figure 31*a* is also from a section through the intorbital septum; this is just a few sections in front of the pituitary fossa. The early invasion of the base of the septum, trabecula communis, by the osteogenetic tissue may be clearly seen here; tiny spicules

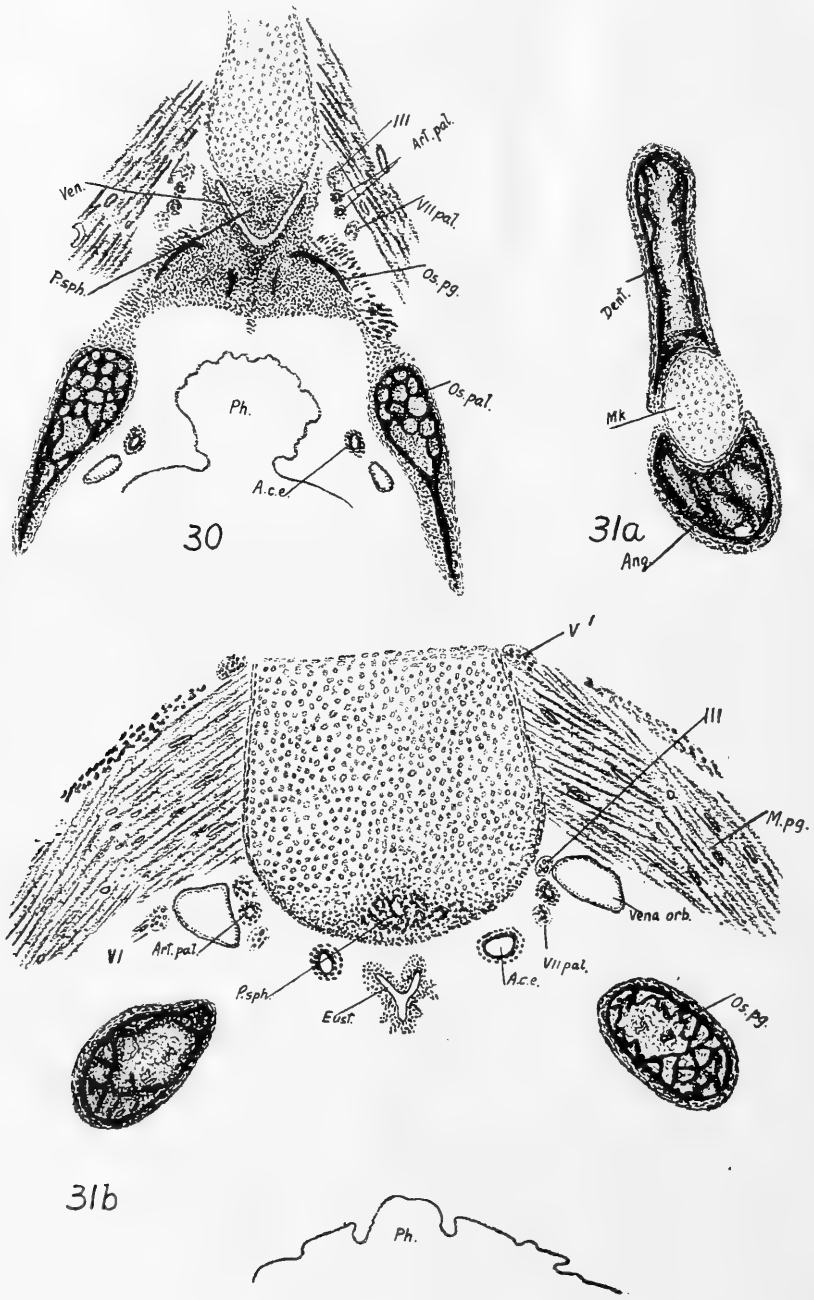


Fig. 30.—*Melopsittacus.* Stage 14 days. A transverse section through the posterior orbital region.

Fig. 31*a*.—*Melopsittacus.* Stage 14 days. A transverse section through the pre-pituitary region. Fig. 31*b*.—Transverse section of Meckel's cartilage and related bones, from the same section.

of bone have already been formed. The advanced development of the pterygoid bone may be contrasted with that of the presphenoid ossification.

Figure 31*b* is taken from Meckel's cartilage and two of its investing bones, and illustrates another feature in the same section as Figure 31*a*.

The clear-cut, unchanged surface of the cartilage in contact with the stromata of the investing bones is in strong contrast with the lower end of the intorbital septum, whereon the endochondral presphenoid is commencing to be formed.

3. The Cormorant, *Phalacrocorax varius* Gmelin (Figs. 32–35).

Stage A.—Head length 21·3 mm. Figure 32, from a section cut through the posterior end of the intorbital septum, shows the proliferation of the perichondrium on both sides of the ventral edge of the cartilage, and the absence of the perichondrium below the cartilage between those areas. There is a general similarity between this ectochondral ossification and that of the two pterygoid bones; actually, however, the osteogenetic membrane around the latter two bones is thicker and its cells, besides being more densely packed, stain more intensely.

Figure 33 is from a section cut through the pituitary fossa in front of the arterial canal. Of interest here, is the continuity between the osteogenetic tissue below the ventral table and the osteogenetic tissue pervading the connective tissue between the cartilages and invading the cartilages themselves. The approximate boundary of the

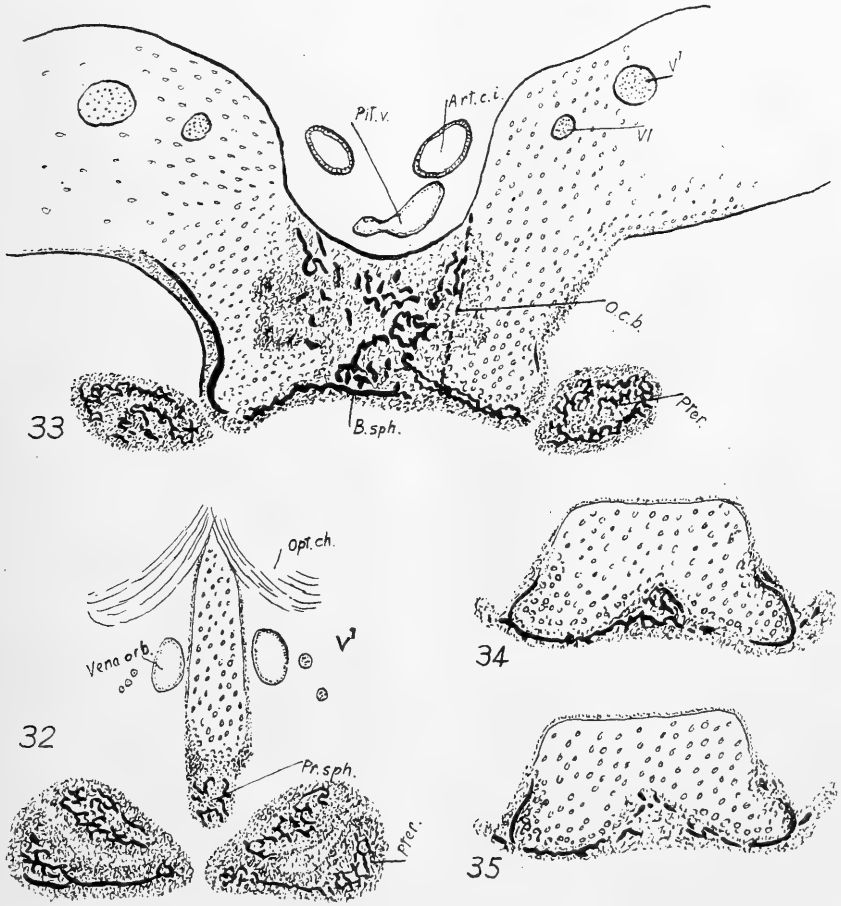


Fig. 32.—*Phalacrocorax*, head length 21·3 mm. A transverse section through the pre-pituitary region.

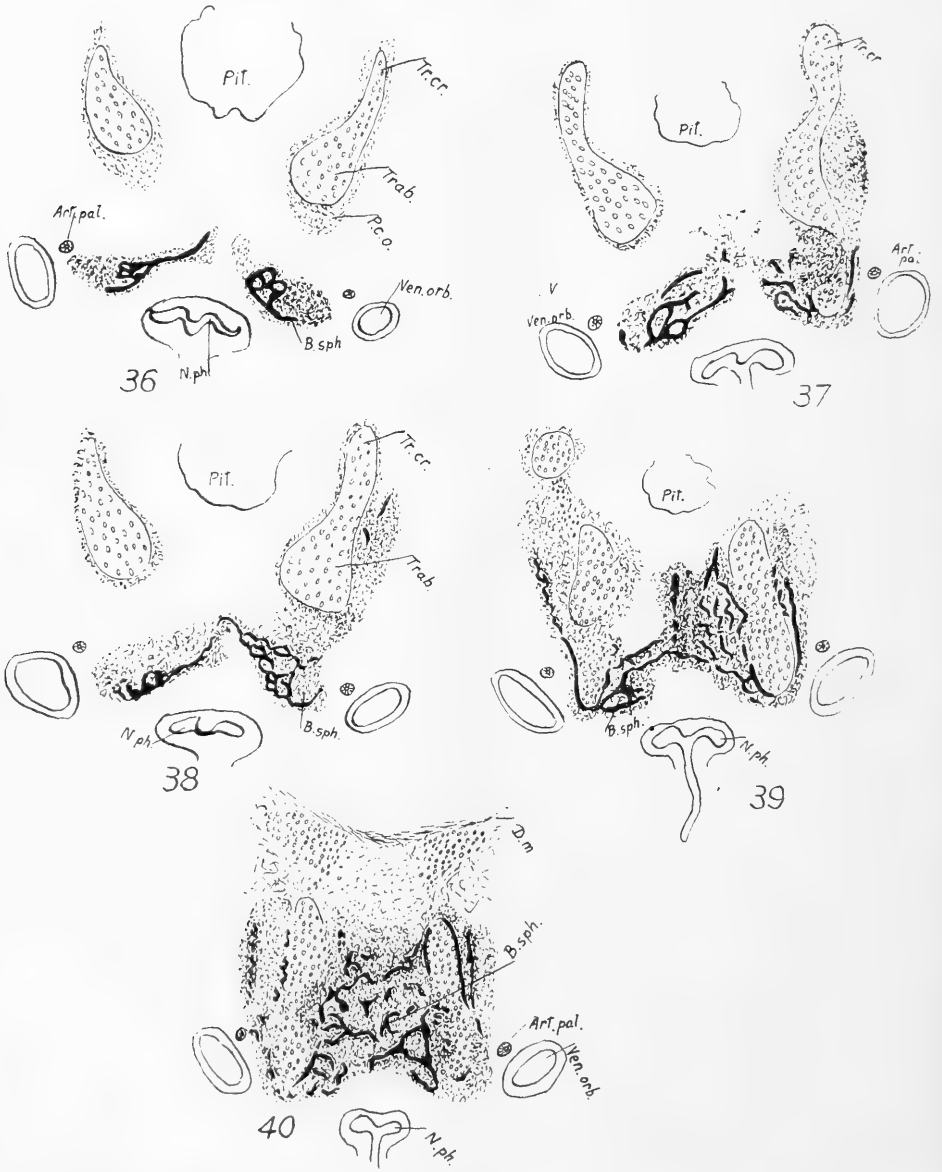
Figs. 33-35.—*Phalacrocorax*. Transverse section through the pituitary and post-pituitary regions.

cartilage on the right-hand side, before the invasion, is indicated by the dotted line *O.c.b.* Other features of interest are the presence of the long bony squame on the ventrolateral surface on the right-hand side, the proliferation of the perichondrium in this area on both sides, and the very definite line of demarcation between the osteogenetic tissue of the true membrane bone, the pterygoid, which makes contact with the cartilage at this point, and that of the basisphenoid.

Figures 34 and 35 show the continuity between the ventral and lateral squames on the surface of the cartilage a little further back.

4. The Chick, *Gallus domesticus* Linné (Figs. 36–40).

Stage, 14½ days' incubation at 38°C.—The sections illustrated are numbers 180 to 176 in my own series of this stage; they provide almost conclusive evidence that there



Figs. 36-40.—*Gallus.* Stage, 14½ days. Five consecutive transverse sections through the pituitary region. Fig. 36 is the hindmost, Fig. 40 the foremost.

is no parasphenoid on the base of this chondrocranium. In the first (Fig. 36) we have the two, so-called, basitemporal bones. These are little squames of bone situated beneath, but at quite a distance from the trabecular cartilages. These sections are each 100μ thick, and in the next (Fig. 37) the cartilage is found to have been not so far distant, at least on the right side, for the section has been cut just behind an abrupt rise dorsad of the postero-ventral surface of the cartilages. In the section next in front of this (Fig. 38) we find complete continuity of the osteogenetic tissue from which the "basi-temporals" are being developed and almost complete continuity between the bones themselves. In the next section (Fig. 39) the bones are joined together in the mid-line and are also continuous with bone which has been deposited on the lateral surfaces of the cartilages and with that which, lying between the cartilages, is invading the one on the right-hand side. In the last section (Fig. 40), as in the fourth, it is quite impossible to define any boundary between two bony elements of different origin.

5. *Apteryx.*

The specimen studied had a head length of 5·5 cm. from tip of snout to the occiput. There was no record as to how far advanced in hatching the chick was, but, since the feathers were but poorly developed, it was probably several days short of the full period. The specimen was one of the collection made by Jeffery Parker many years ago, when he was studying the development of the bird. Notwithstanding its age the preservation was almost perfect.

It was stained in bulk and embedded in nitrocellulose. It was then sectioned to the mid-line in the sagittal plane and then remounted and the remaining half cut transversely. A model of the portion we are interested in was reconstructed from these transverse sections.

For this model the drawings were made directly on white blotting paper. After they were cut out, the portions of cartilage undergoing ossification, already indicated on the drawing, were coloured red, the nerves and the Gasserian ganglion were coloured blue, and the cerebral artery dark purple. The drawings were then dipped into paraffin and placed in position before the paraffin cooled.

It was found that the basisphenoid bone had apparently commenced ossification from two centres, ectochondrally and ventrally. This appeared to explain the fact that the basisphenoid region of the chondrocranium was found to be permeated by endochondral ossification throughout its thickness on each side of and slightly behind the pituitary fossa. The upper limit of this ossification was found to fall away ventrad, posteriorly and anteriorly. The whole of the floor of the fossa was ossified, as also was the lateral wall in front of the arterial foramen. This ossification of the cartilage permeated, not only the vertical, but also the lateral thickness of it in this region, and extended out along the remarkably massive basipterygoid boss so that only the core and extreme tip of this latter remained as cartilage. Where the cerebral artery enters its canal it lies between cartilage in front and bone behind, but at its point of emergence into the skull it has bone in front and cartilage behind it. This cartilage behind the artery is continuous with the core of the basipterygoid process. At the periphery of this area of ossification there was found only the thin ventral table of the bone. That this was the ventral table, and not a separate basi-temporal ossification, appeared quite definite from the fact that it was quite continuous with the ventral table below the area of more massive ossification; moreover, this lamellar extension of the bone was definitely intra-perichondral at its edge.

No trace of any extra-perichondral ossification was found anywhere on the base of this chondrocranium.

The prootic bone was found to have commenced ossification in its upper and anterior region, and this ossification was in all respects similar to that of the basisphenoid.

The basioccipital, not included in the model, was also found to be ossifying in a similar manner.

If, as believed, the basisphenoid bone commenced ossifying ectochondrally from two ventrally-situated centres, then it is possible that, at an earlier stage than that studied, the appearances might simulate separate basitemporal squames. In view of their

early complete fusion with the endochondral ossification and their situation above the perichondrium, it would surely be erroneous to identify them as parasphenoidal ossifications.

Besides the four avian embryos which have been selected for special description and illustration, embryos of the following birds have been carefully examined for the present study. All these so closely resemble one or other of those selected that it was felt their description and/or illustration would be merely duplication: *Fulica atra* Linné, two stages, *Recurvirostra novaehollandiae* Vieillot, three stages, *Podiceps* sp., *Thraskiornis molucca* Cuvier, one stage, *Botaurus poecilloptilus* Wagler, one stage, *Acrocephalus australis* Gould, eight stages, *Himantopus leucocephalus* Gould, two stages, *Erythrogonys cinctus* Gould, three stages, *Podargus* sp., two stages, *Iredipara gallinacea* Temm., two stages, and *Anas*, twelve stages.

I had expected to include studies of the development of the osteocranium of the Crocodile. Arrangements had been made for the collection of the necessary material but unfortunately on both occasions the district selected for the collection was visited by disastrous floods, which made collection impossible.

Summary.

Very complete series of embryos of two Lacertilia, one Chelonian and three Aves as well as single embryos and/or incomplete series of embryos of twenty other Saurians have been obtained and prepared for microscopical examination during the last ten years.

A careful examination of this mass of material has been carried out, and from it embryos of fourteen Saurian species have been selected for description and illustration.

These reveal that—except for a squame of very fleeting independence, which is present below the pituitary fontanelle of a majority of Lacertilian and Chelonian embryos—there is no structure which can be identified as a parasphenoid bone.

There is strong reason to believe that the tiny squame referred to is an intramembranous extension of that endo-perichondral ossification which was observed to initiate the ossification of the chondrocranium of all Saurians except the Ophidia.

In those reptiles in which the ossification of the basisphenoid commences with the appearance of this squame, it differs in no way from the ossification of the basioccipital bone, which commences with the appearance of a precisely similar squame below the basicranial fontanelle.

Throughout the birds a triangular endo-perichondral squame develops in contact with the cartilage on the base of the skull and in cellular osteogenetic tissue derived, it is believed, from the perichondrium by proliferation of its deep layer.

This triangular squame very rapidly becomes fused with the endochondral bone which develops in the cartilage above it, so that, still quite small, its first-formed portion has already so fused whilst the peripheral portion of the squame has yet to be developed.

Similar squames to this basal one are developed in other relations to the chondrocranium, and in the case of the basisphenoid there are four such others. Therefore, since they *are* all similar, if any be membrane bones, all must be, and under such an interpretation the basisphenoid bone must be deemed to have been formed by the fusion of five membrane bones and one endochondral bone.

This last suggestion is, of course, a *reductio ad absurdum*, and the truth is that the parasphenoid is developed from five similar endo-perichondral centres of ossification.

Conclusion.

The tiny squames on the base of the chondrocrania of various Saurians, which have been identified as parasphenoidal ossifications, are in reality endo-perichondral ossifications, and no true parasphenoid bone is found on the base of any Saurian skull.

It follows that, in the Saurians the parabasal canal is enclosed by the basisphenoid bone only; except in the Chelonians, where part of its floor is supplied by the pterygoid bone.

These findings support my belief and contention that the reptilian pterygoid bone should be equated with the lateral wings of the amphibian parasphenoid bone.

This equation was first advanced in 1916 (Kesteven, 1916)* and leads on to the equation of the mammalian pterygoids with the reptilian pterygoids and with the same lateral wings of the amphibian bone, an interpretation which was advanced at the same time and which has been supported by several communications since (Kesteven 1919 to 1931) and which has recently been adopted by de Beer on portion only of the evidence advanced in those communications.

* A list of references to literature is not given here because all but certain of my own communications are listed in de Beer's very fine list at the end of his book on "The Development of the Vertebrate Skull". My own communications were printed in the *Journal of Anatomy* and in the *Records of the Australian Museum*. Cayley's book, referred to in a previous footnote, was published by Angus & Robertson, Sydney.

NEW AND KNOWN NEMATODES FROM AUSTRALIAN MARSUPIALS.

By T. Harvey Johnston and Patricia M. Mawson, University of Adelaide.

(Thirty-four Text-figures.)

[Read 30th October, 1940.]

Material from various parts of Australia, chiefly from New South Wales and Queensland, has been examined and amongst it were found, in addition to many previously described forms, eight new species, the allotype male of one hitherto incompletely described, and the allotype females of two others. For much of it we are indebted to the late Dr. T. L. Bancroft, Eidsvold, Upper Burnett River, Queensland; Professor J. B. Cleland; Messrs. L. Gallard, Ourimbah, Gosford district, N.S.W.; A. S. Le Souef, Director, Sydney Zoological Gardens; the Tasmanian Biological Survey; and the South Australian Museum. Where not otherwise indicated, the material was collected by the senior author. The investigation was made possible by the Commonwealth Research Grant to the University of Adelaide. Types of new species and the allotypes have been deposited in the South Australian Museum, Adelaide.

A complete list of the material examined and the parasites identified would be largely a repetition of previous findings; consequently in this account only new host records and new species are mentioned. The following is a list of the newly-recorded nematodes arranged under their hosts:

Lagorchestes hirsutus Gould: *Zoniolaimus communis* J. & M.

Macropus dorsalis Gray: *Pharyngostrongylus theta* J. & M., *Cloacina similis* J. & M., *C. digitata*, n. sp., *Zoniolaimus longispicularis* (Wood).

Macropus fuliginosus Desm.: *Dipetalonema roemeri* (Linst.).

Macropus major Shaw: *Cloacina communis* J. & M.

Macropus parma Waterhouse: *Parazoniolaimus collaris* J. & M., *Pharyngostrongylus alpha* J. & M., *P. gamma* J. & M., *P. delta* J. & M., *Coronostrongylus coronatus* J. & M., *Cloacina thetidis* J. & M., *Buccostrongylus buccalis* J. & M.

Macropus robustus Gould: *Pharyngostrongylus beta* J. & M.

Macropus ruficollis Desm.: *Cloacina linstowi*, n. sp., *C. similis* J. & M., *C. thetidis* J. & M., *Coronostrongylus coronatus* J. & M.

Macropus tasmaniensis Le Souef: *Zoniolaimus longispicularis* (Wood).

Macropus thetidis Lesson: *Zoniolaimus onychogale* J. & M., *Cyclostronglus medioannulatus*, n. sp., *Dipetalonema* sp.

Macropus ualabatus Less. & Garn.: *Cloacina gallardi*, n. sp., *Globocephaloides thetidis* J. & M., *Austrostrongylus aggregatus*, n. sp.

Peragale minor Spencer: *Subulura peragale*, n. sp., *Physaloptera thalacomys*, n. sp.

Perameles nasuta Geoffr.: *Physaloptera parvicollaris*, n. sp., *Echinonema cinctum* Linst., *Dipetalonema* sp.

Sarcophilus harrisi Boitard: *Physaloptera sarcophili*, n. sp.

Trichosurus caninus Ogilby: *Dipetalonema trichosuri* (Breinl).

? Bandicoot (*Echymipera* sp. or *Peroryctes* sp.): *Physaloptera papuensis*, n. sp.

New Host Records for Known Species.

The following parasites were found in hosts from which they had not previously been recorded:

Buccostronglus buccalis J. & M. from *Macropus parma* (Ourimbah, N.S.W.); *Cloacina communis* J. & M. from *M. major* (N.S.W.); *Cloacina thetidis* J. & M. from *M. parma* (Ourimbah), *M. ruficollis* and *M. wilcoxi* (Burnett R.); *Cloacina similis* J. & M. from

M. dorsalis, *M. ruficollis* and *M. wilcoxi* (Burnett R.); *Parazoniolaimus collaris* J. & M. from *M. parma* (Ourimbah); *Pharyngostronglus alpha* J. & M. from *M. parma* (Ourimbah); *Pharyngostrongylus beta* J. & M. from *M. robustus* (N.S.W.—Sydney Zoological Gardens); *Pharyngostrongylus delta* J. & M. from *M. parma* (Ourimbah); *Pharyngostrongylus theta* J. & M. from *M. dorsalis* (Burnett R.); *Zoniolaimus longispicularis* (Wood) from *M. dorsalis* (Burnett R.) and *M. tasmaniensis* (Tasmania); *Zoniolaimus onychogale* J. & M. from *M. thetidis* (Burnett R.); *Zoniolaimus communis* J. & M. from *Lagorchestes hirsutus* (Western Australia—Adelaide Museum); *Zoniolaimus* sp. from *M. parma* (Ourimbah); *Dipetalonema trichosuri* (Breinl) from *Trichosurus caninus* (Narara, N.S.W.); and *Dipetalonema roemeri* (Linst.) from *M. fuliginosus* (Kangaroo Island).

Cloacina digitata, n. sp. Figs. 1–4.

Very common in the stomachs of three specimens of *Macropus dorsalis*, Burnett River (coll. T. L. Bancroft). Fairly robust worms, males 4–5 mm., females 4·8–8·7 mm. long. Six shallow lips, each submedian with papilla 12μ long and consisting of two joints, upper very small; each lateral lip with small conical papilla. Buccal capsule 0·02 mm. wide, chitinous walls thin, 0·09 mm. deep. Oesophagus 0·45 mm. long (1:9·5 of body length) in male, 0·48 mm. (1:19 of body length) in female 8·7 mm. long. Nerve ring 0·2 mm., and excretory pore 0·4 mm. from anterior end. Cervical papillae thread-like, 0·04 mm. long, 0·11 mm. from head end.

Male. Bursa large, not deeply lobed, ventral lobes continuous. Ventral rays stout but tapering, cleft half their length; externo-lateral very stout, divergent from laterals; laterals cleft nearly all their length; externo-dorsal arising separately, its tip raising bursal wall; dorsal bifurcating just before its mid-length, each branch ending in two short stout branches; none of the bursal rays reaching bursal edge. Genital cone short, pointed. Spicules 2·1 mm. long (half body length).

Female. Body narrowing posterior to vulva, and ending in thin pointed tail with dorsally-directed tip; vagina fairly short, twisted; vulva 0·2 mm. and anus 0·11 mm. from tip of tail. Eggs 0·1–0·12 mm. by 0·05–0·06 mm. The head of this worm most closely resembles those of *Cloacina elegans* and *C. curta*. It differs from the former in having lips, in the lengths of spicules and vagina, and in the position of nerve ring; and from *C. curta* in the shape of oval papillae, bulb on the posterior end of the oesophagus, and in the length of cervical papillae, spicules and vagina. The specific name has reference to the finger-like form of the submedian papillae.

Cloacina linstowi, n. sp. Figs. 5–7.

From *Macropus ruficollis*, Burnett River (coll. T. L. Bancroft).

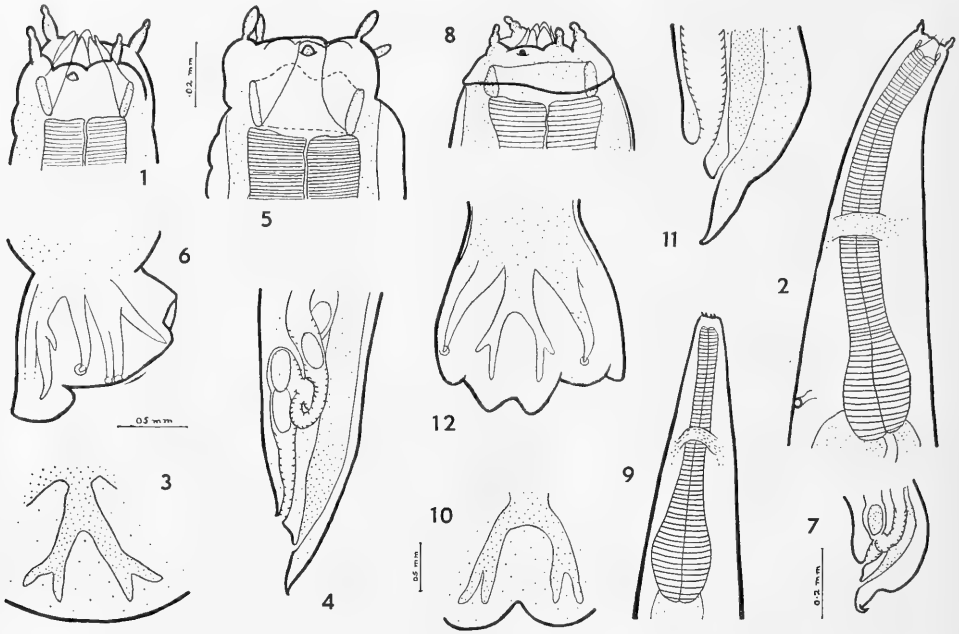
Short stout worms, female 3·4 mm., male 2·4 mm. long. Anterior end surrounded by wide collar bearing six lips; lateral lips each with small conical papilla; submedian each with papilla (10μ long in male) of unusual shape, the base being short and the distal segment very long and thin. Buccal cavity deep, base 0·03 mm. from top of lips; buccal ring 4μ thick, 27μ wide at base, slightly wider at top, and with wavy anterior edge so that depth varies from 14μ to 20μ. Oesophagus in female 0·35 mm. long, ending in bulb. Position of nerve ring in all specimens obscured. Excretory pore in region of third quarter of oesophageal length. Cervical papillae 40μ from anterior end.

Male. Spicules 0·62 mm. long (1:4 of body length). Bursa longer at dorsal than ventral lobes. Ventral rays parallel; externo-laterals reaching bursal edge, divergent from laterals; laterals cleft half length; externo-dorsals arising separately and shorter than laterals; tips of laterals and externo-dorsals directed laterally and elevating bursa. Dorsal ray dividing at end of first quarter, each branch giving off short lateral soon after origin, and neither branch reaching bursal edge.

Female. Body narrowing suddenly beyond vulva and ending in pointed tail, 0·13 mm. long. Vagina very short; vulva 0·18 mm. from posterior end. Eggs in uteri 90μ by 50μ.

The species differs from other members of the genus in the shape of the submedian papillae, the deep buccal capsule, and the dorsal ray of bursa. In the latter feature, in the shape of the papillae, and in the possession of wavy anterior edge of buccal capsule,

this worm very closely resembles *Cloacina dahli*, described by Linstow from *Macropus browni* from New Britain, but differs in the depth of buccal capsule, and in shorter vagina. These differences, combined with very different geographical range of the hosts, are sufficient to distinguish between the two species.



Figs. 1-4.—*Cloacina digitata*. 1, head; 2, anterior end; 3, dorsal rays; 4, posterior end of female. Figs. 5-7.—*Cloacina linstowi*. 5, head; 6, bursa; 7, posterior end of female. Figs. 8-11.—*Cloacina gallardi*. 8, head; 9, anterior end; 10, dorsal ray; 11, posterior end of female. Fig. 12.—*Cloacina thetidis*, bursa. Figs. 1 and 5 drawn to same scale; figs. 2 and 10; figs. 3, 6, 8, and 12; figs. 4, 7, 9, and 11.

CLOACINA GALLARDI, n. sp. Figs. 8–11.

From stomach of *Macropus ualabatus*, Ourimbah, N.S.W. (coll. L. Gallard).

Large worms; males 11–12 mm., females about 13–15 mm. in length. Head with definite collar bearing six lips; submedian papillae of two almost equal joints, rather short; lateral papilla small, conical. Buccal ring large, stouter at base than anterior by 0·08 mm. wide, 0·023 mm. deep, base 0·04 mm. from top of lips, and anterior margin forming a wavy line. Oesophagus 0·82 mm. long in male (1:14 of body length), surrounded by nerve ring at about mid-length, then widening into a slight bulb succeeded by a larger bulb before joining intestine. Cervical papilla about 0·18 mm. from anterior end of worm; excretory pore in region of oesophageal bulb.

Male. Bursa large, lobes not deeply separated from one another. Ventral rays parallel, reaching edge of bursa; externo-lateral and externo-dorsal arising with laterals, but divergent from them, each lifting up lateral wall of bursa a short distance from bursal edge. Laterals cleft nearly all their length, not reaching edge of bursa. Dorsal ray stout, bifurcating near root, branches divergent and each dividing after two-thirds length into two equal rays not reaching edge of bursa. Spicules very long, nearly two-thirds body length. Genital cone large; accessory cone formed by pair of elongate processes.

Female.—Tail pointed, 0·2 mm. long; ovejections 0·4 mm. long, uniting about 1·4 mm. in front of vulva. Vagina twisted; vulva 0·07 mm. in front of anus.

This species resembles *C. longispiculata* J. & M. (1939) in many features, but differs mainly in the form of the dorsal ray and in the absence of a cuticular inflation at the anterior end of the body. It is also very like *C. magnipapillata* J. & M. (1939) but differs

in having a more definite oesophageal bulb, deeper buccal capsule, smaller papillae, and simple tips to the elements of the leaf crown.

CLOACINA THETIDIS Johnston & Mawson 1939*b*. Fig. 12.

This species was described from a female specimen from *Macropus thetis*. Among numerous other worms in the stomach of *Macropus parma* from Ourimbah a male worm was found, agreeing in the structure of the head and oesophageal region with the type female of *C. thetidis*.

The six inner lips each bear an element of the leaf crown as was suggested in the earlier description. Male 4 mm. long. Oesophagus 0·56 mm. in length (1:7 of body length). Spicules very short, 0·48 mm. long, 1:8·3 of body length, broad, with very wide striated alae. Bursal lobes not deeply separated from one another. Ventral rays thin, parallel, cleft for most of length; externo-lateral diverging from laterals at base; laterals parallel, cleft for half length; externo-dorsal arising at base of laterals and its tip raising wall of bursa; dorsal stout, bifurcating at mid-length, each branch giving off a short lateral at about its mid-point. None of the rays reaches the edge of the bursa.

CYCLOSTRONGYLUS MEDIOANNULATUS, n. sp. Fig. 13.

From stomach of *Macropus thetis*, Burnett River.

Three females were found, the longest 5 mm. Mouth collar with four double submedian papillae and two larger lateral papillae, each submedian with bifid bristle. Buccal cavity 25μ deep, 31μ wide, supported about mid-length by ring of chitin 5μ deep. Oesophagus cylindrical, narrow, widening suddenly into small terminal bulb at 0·73 mm. from anterior end of head. Excretory pore 0·4 mm. from head end. Tail 0·28 mm. long, ending in narrow point. Vagina 0·3 mm. long; the vulva 0·12 mm. in front of anus. Eggs 40–50μ by 60–70μ.

The worms differ from other Cyclostrongyles in having only a narrow supporting ring around buccal cavity. In this respect they resemble members of the genus *Maplestonema*, but the presence of a cuticular roll around mouth and the difference between the four submedian and the two lateral oval papillae suggest the species belongs to *Cyclostrongylus*. The specific name has relation to the position of the thickened ring in the buccal cavity.

CORONOSTRONGYLUS CORONATUS J. & M. 1939*a*. Figs. 14–15.

This species was described from two indifferently preserved specimens, a male from *Macropus wilcoxi*, and a female from *M. thetis*. Several more satisfactory specimens have now been obtained from *M. parma* (Ourimbah) and *M. ruficollis* (Burnett River), although the parasite apparently occurs rarely. We now offer an emended description.

Oesophagus in male 3·6 mm. long, is 0·42 mm. long, 1:8·7 of body length, straight, cylindrical anteriorly, ending in a bulb. Spicule 0·75 mm. long, 1:5 of body length—this difference from the type being probably due to its unwrinkled state. Lobes of bursa deeply separated from one another as in *Pharyngostrongylus*; ventral and lateral lobes covered on their inner surface with irregular papillae. Ventral rays parallel; externo-lateral short, its tip lifting wall of bursa; laterals long, parallel; externo-dorsal arising separately, shorter than laterals, its tip elevating wall of bursa. Dorsal ray very stout, dividing at mid-length into pair of thin branches medially and a pair of short, very wide lateral rays, none of the branches reaching bursal edge. Gubernaculum small, heart-shaped in dorsal view: pair of prebursal papillae, 0·03 mm. in front of anterior end of bursa; genital cone prominent.

In the female the two ovejectors unite to form a vagina 0·32 mm. long. Anus 1 mm. behind vulva and 0·35 mm. from tip of tail. Eggs 60–70μ by 30–40μ.

GLOBOCEPHALOIDES THETIDIS J. & M.

The species was described from a single male worm from the intestine of *Macropus thetis*, Burnett River. Amongst our present material is a female from the duodenum of *Macropus ualabatus*, Milson Island, agreeing in the characters of the head with that male. Length 9·6 mm.; oesophagus 0·76 mm. long, 1:12·6 of body length; vulva 3·3 mm. from

posterior end of worm, its position marked by a small flap of the body wall. Tail conical. Eggs 76–80μ by 33–40μ.

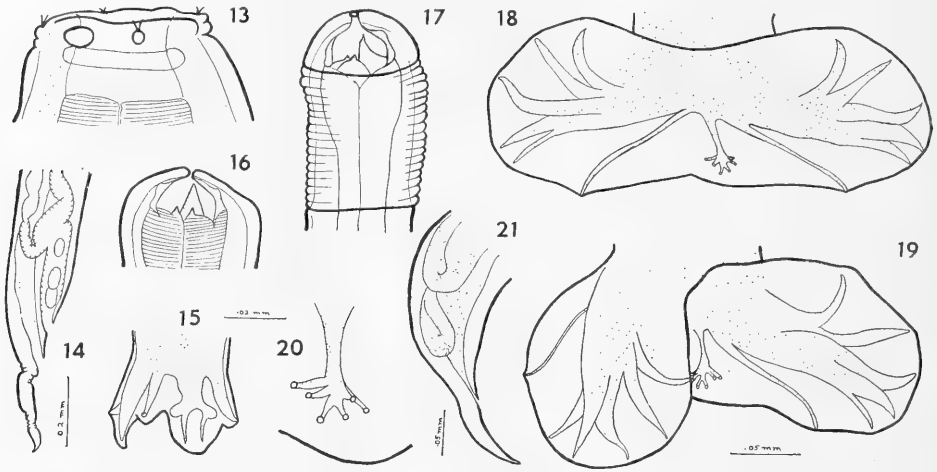


Fig. 13.—*Cyclostrongylus medioannulatus*, head. Figs. 14-15.—*Coronostrongylus coronatus*. 14, posterior end of female; 15, bursa. Figs. 16-21.—*Austrostrongylus aggregatus*. 16, head, dorsal view; 17, anterior end, lateral view; 18, bursa opened wide; 19, more natural position of bursa; 20, dorsal ray; 21, posterior end of female. Figs. 13, 16, 17, and 20 to same scale; figs. 15, 18, and 19.

AUSTROSTRONGYLUS AGGREGATUS, n. sp. Figs. 16–21.

From the duodenum of *Macropus ualabatus*, Milson Island, Lower Hawkesbury, N.S.W. (coll. J. B. Cleland). The worms are very tightly coiled in five or six spirals. Length 3–4 mm. Anterior end surrounded for the first 0·06 mm. of its length by inflated cuticle which, unlike that of the type species, is transversely striated. Remainder of body with two wide lateral and four narrower submedian longitudinal, transversely-striated crests, the laterals continuing as far as vulva in female, the left lateral as far as bursa in male. Buccal capsule 15μ deep, and 20μ wide at base (including the strongly chitinized walls). Dorsal tooth 10μ long; a pair of short subventral teeth present. Oesophagus 0·29 mm. long.

Male.—Spicules very thin, 0·7 mm. long, 1:5 of body length. Bursa large, symmetrical, otherwise similar to that in other species of genus. Externo-dorsal is the only ray reaching bursal edge; all rays directed ventrally at extreme tips. Dorsal ray bifurcating near tip, giving off two pairs of lateral branches just proximal to bifurcation, all branches of dorsal ray appearing to bend ventrally in the bursal wall so that their apparent length in the figure is shorter than their actual length.

Female. Body narrowing suddenly just anterior to anus, then again 20μ before tip, so that end of tail is spine-like. Anus at 0·09 mm. and vulva at 0·4 mm. from posterior end.

The specific name has reference to the closely-grouped branches of the dorsal ray. The species differs from *A. macropodis* Chandler in having a pair of ventral teeth, in the length of spicules, in the symmetry and width of the bursa, and in the length and form of the dorsal ray. It is nearest to *A. wallabiae* J. & M., differing in size and in the shape of the buccal capsule and dorsal tooth, the presence of two ventral teeth, longer spicules, the arrangement of the bursal rays, and the position of vulva, as well as in the absence of masses of granular tissue in bursa and near vulva described for *A. wallabiae*.

SUBULURA PERAGALE, n. sp. Figs. 22–24.

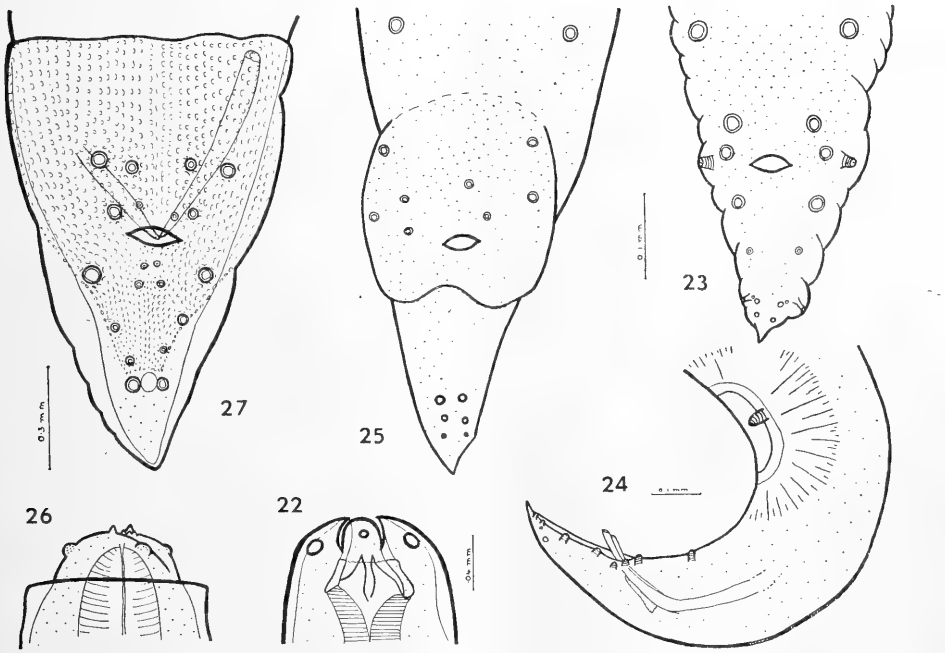
From the stomach of *Peragale minor*, from MacDonald Downs, Central Australia. Males 9–10·6 mm. long; females 13–15 mm. Anterior end with six lips; four submedians each with a large papilla, two laterals each with a smaller papilla. Buccal cavity

0·06 mm. deep, widest at base (diameter 0·05 mm.), posterior half of buccal cavity most strongly chitinized; at junction of this part with the thickened cuticle on inner edges of lips a ring of short vertical striations perhaps due to change in density of the walls. Three large teeth arising from anterior end of oesophagus, and provided with long sharp points reaching half-way up buccal cavity. Oesophagus typical in form, 1·95 mm. long (in a male 10·6 mm. long), with bulb almost spherical, 0·2 mm. in diameter. Nerve ring at 0·4 mm., and the excretory pore at 0·55 mm. from anterior end of worm.

Male. Spicules narrow, 2·9 mm. long, 1:4 of body length. Cloaca 0·21 mm. from tip of tail. Eleven pairs of papillae, of which three pairs are precloacal, two pairs at level of cloaca, and six pairs postcloacal. Gubernaculum present.

Female. Tail elongate, tapering, 0·8 mm. long; vulva 5 mm. from anterior end in worm 14·7 mm. long, i.e. 1:3 of body length from head end. Eggs subglobular, 60–70μ in diameter.

The species differs from *S. peramelis* Baylis in having six, instead of twelve, lips, in the absence of accessory teeth, and in having eleven instead of ten pairs of cloacal papillae in the male.



Figs. 22-24.—*Subulura peragale*. 22, head; 23, posterior end of male, ventral view; 24, posterior end of male, lateral view. Fig. 25.—*Echinonema cinctum*, posterior end of male, ventral view. Figs. 26-27.—*Physaloptera thalacomys*. 26, head; 27, bursa. Figs. 23, 25 and 27 to same scale.

Echinonema cinctum Linstow. Fig. 25.

Three females and two males of this species were obtained from the intestine of *Perameles nasuta* from Sydney. They agree very well with the descriptions given by Linstow and by Yorke and Maplestone, except in regard to the male tail. Yorke and Maplestone state that there are no caudal alae. We notice that just posterior to the cloaca there is an expansion of the body which is very like caudal alae except that it is less transparent. The structure merges into the rest of the body about 0·15 mm. in front of cloaca. We have also noted more papillae in this region than were recorded by Yorke and Maplestone. There are in our specimens three pairs near the tip of tail, two pairs just antero-lateral to the cloaca and two pairs lateral to these, one of these pairs being at the upper edge and the other pair about half-way down the expansion of the

body, described above. About 0·25 mm. in front of cloaca is another pair of larger papillae. The group of very small papillae mentioned as occurring near the tip of the tail was not observed.

PHYSALOPTERA THALACOMYS, n. sp. Figs. 26-27.

From the stomach of *Peragale minor*, MacDonald Downs, Central Australia. Stout worms; males up to 2·4 cm.; females to 3·8 cm. long. Cervical collar reaching base of lips; head of female 0·13 mm. across at base of lips; each lip with two large submedian papillae and on its inner edge bearing two median teeth, an inner tripartite and a larger conical external. Oesophagus in male, 5·3 mm. long, muscular part 0·5 mm. long. Nerve ring 0·4 and the excretory pore 0·7 mm. from head end.

Male. Bursa elongate, 1·3 mm. long, 0·6 mm. wide across cloaca, 0·85 mm. wide anteriorly. Spicules not heavily chitinized, one about 0·65 mm. long, the other indistinct and either 0·35 mm. or 0·67 mm. long. Ten pairs of bursal papillae, four pairs preanal and six pairs postanal, arranged as shown in Figure 27. Between the two most posterior pairs of papillae is a structure which may be another papilla but whose outline is not so strongly marked. Small tubercles, arranged for the most part in longitudinal rows, extend over the precloacal part of bursa and are continued over middle part of the tail nearly to the last pair of papillae, leaving each ala free.

Female. Didelphous; vulva 9 mm. from head. Tail rounded, 0·35 mm. long in a 3·8 cm. specimen, and bearing a pair of rounded shallow subterminal ventral papillae. Eggs in vagina 30μ by 45μ.

The species differs from *P. peramelis* J. & M. (from *Perameles nasuta*) in having a long narrow bursa rather than a short wide one, in the position of the excretory pore, and in the number and arrangement of the caudal papillae in the male. It resembles *P. peragale* J. & M. (also from *Peragale minor*) in the size and shape of the bursa, but differs in the number of bursal papillae, the position of the excretory pore, the shape of the female tail, and in the more anterior position of vulva. These three latter are the most striking differences, as the bursal papillae observed in *P. peragale* are irregular in arrangement and probably atypical. The specific name is derived from *Thalacomys minor*, an alternative name of the host.

PHYSALOPTERA SARCOPHILI, n. sp. Figs. 28–29.

From the Tasmanian Devil, *Sarcophilus harrisi*, Tasmanian Biological Survey. Two females, 23 and 13 mm. long, and a male 11 mm. long, were present. Cervical collar wide and loose; in the two shorter specimens covering bases of lips, in the longer reaching nearly to top of lips. Outer tooth on each lip slightly longer than the tripartite median tooth.

Male. Bursa very large, alae thin and much wrinkled, 2 mm. long, 1·2 mm. maximum breadth. Tail 1·1 mm. long. Four pairs long pedunculated papillae (two pairs preanal and two pairs postanal) and three pairs short papillae on medio-ventral surface of tail (as in fig. 29). Spicules very narrow, the wider 0·45 mm., the other 0·7 mm. long.

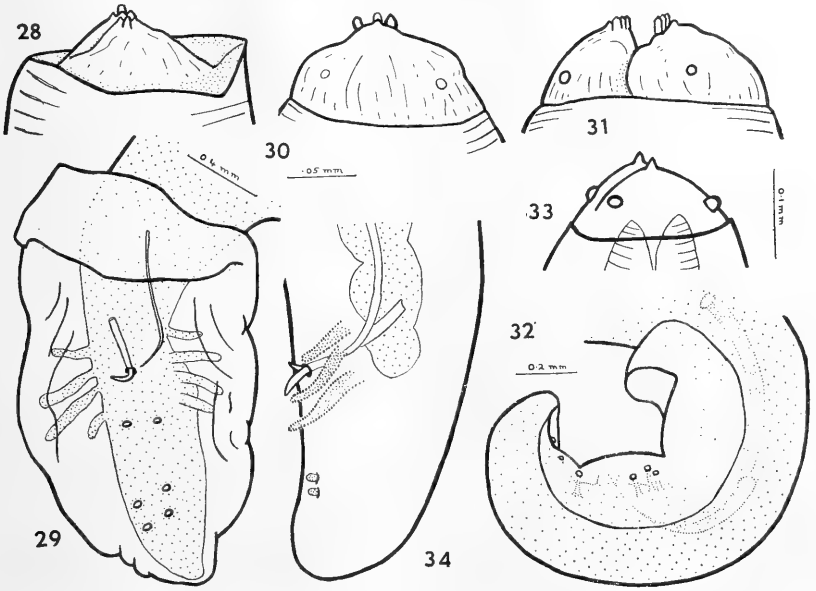
Female. Vulva at one-third length of body from anterior end. Tail rounded at tip; 0·3 mm. long in female 13 mm. long.

PHYSALOPTERA PARVICOLLARIS, n. sp. Figs. 30–32.

From *Perameles nasuta*, Sydney. Two worms present, a male 14·6 mm. and a female 16·3 mm. in length. Collar much reduced, being merely a ridge at base of lips. Each lip with three large median teeth and a shorter tooth external to these; a pair of small papillae on each lip. Oesophagus 4 mm. long in male, anterior part 0·5 mm. long. Nerve ring 0·4 mm. from head end.

Male. The only specimen was so twisted that a view of the ventral caudal region could not be obtained, hence the description of the papillae is incomplete. In lateral view there were seen three pairs of pedunculated precloacal papillae, one more medially situated than the other two, one pair of pedunculated post-cloacal papillae, and two pairs of short papillae situated between the cloaca and the tip of tail. Tail 0·4 mm. long. Spicules not well seen even in creosote, one 0·47 mm. and the other probably 0·8 mm. long.

Female. Tail bluntly rounded; vulva 6·9 mm. from anterior end, 1:2·4 of body length from head.



Figs. 28-29.—*Physaloptera sarcophili.* 28, head, lateral view; 29, bursa, ventral view. Figs. 30-32.—*Physaloptera parvicollaris.* 30, head, lateral view; 31, head, ventral view; 32, bursa, lateral view. Figs. 33-34.—*Physaloptera papuensis.* 33, head; 34, posterior end of male. Figs. 30 and 31 to same scale; figs. 28 and 33; figs. 32 and 34.

Physaloptera papuensis, n. sp. Figs. 33–34.

These worms were obtained from a mammal collected at Mount Lamington, Papua, by Mr. D. McNamara and forwarded to the South Australian Museum. The identification of the host is uncertain but evidence points to it being a bandicoot. The native name, partly defaced on the label containing the parasites, appears to be Masia.

The females are very long, young ones 2·4 cm., older up to 6 cm.; males about 2–3 cm. All specimens very poorly preserved. Lips extending above the level of the collar; each with large median tooth and possibly two lateral. Four large submedian papillae. Nerve ring towards base of muscular part of oesophagus, 0·55 mm. from anterior end of worm. Posterior end of all males very macerated, extent of alae indeterminable, and ventral view unobtainable. Five pairs of pedunculate papillae, three preanal and two shorter postanal, can be seen; one specimen shows four preanal. There are also one pair preanal and two pairs immediately postanal sessile papillae, and there may be more towards posterior end. Spicules straight, tapering to a point, longer and thinner spicule 0·7 mm., shorter 0·35 mm.

Female.—Vulva dividing body antero-posteriorly in ratio 2:3.

This species differs from those known from marsupials in its much greater length and in the number and position of the cloacal papillae. The geographical distribution of the hosts is quite different.

Dipetalonema sp.

From lung of *Perameles nasuta*, Sydney. All the worms are broken and in a poor state of preservation so that their structure is difficult to make out. All the pieces present belong to females and are filled with larvae. Maximum width 0·35 mm. Head 0·03 mm. diameter, with four, possibly six, papillae. Small mouth leading to tubular vestibule 0·01 mm. long followed by oesophagus 0·26 mm. long, latter apparently short in relation to body length. Tail 0·1 mm. long, conical, tip ending in a narrow point. Vulva a short distance behind oesophagus.

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NOTES ON THE SYNONYMS OF *TROMBICULA MINOR* BERLESE 1904.

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

[Read 25th September, 1940.]

Much discussion and explanation can be avoided if the relevant facts are set out in chronological order:

1904. Berlese described *T. minor* (nymph or adult, from an imperfect specimen) from Java.
1912. Berlese described *T. mediocris* (adult), also from Java.
1916. Tanaka described *T. pseudoakamushi* from Japan.
1918. Kitashima and Miyajima reported *Leptus autumnalis* Shaw 1790 from Formosa.
1919. Hatori reported a new species from Formosa which he named "*T. pseudoakamushi*".
1920. Miyajima stated that *T. minor* was the nymph of *T. mediocris* (or vice versa; both versions exist).
1921. Kawamura and Yamaguchi reported *T. pseudoakamushi* Hatori from Formosa, and suggested that it was the larva of *T. mediocris*.
1923. Walch reported *T. pseudoakamushi* Hatori from Sumatra, on man but not on rats.
1924. Walch referred to the Sumatran species as "*T. pseudoakamushi* (variatio *deliensis*)".
1925. Walch referred to the Sumatran species as "*T. pseudoakamushi* (variatio *deliensis* ?)", and stated that its nymph very closely resembled both *T. mediocris* and (with certain differences) the nymph of *T. pseudoakamushi* (Kawamura and Yamaguchi) from Formosa.
1927. Walch reported *T. pseudoakamushi* Hatori on rats from Sumatra and Macassar.
1927. Sambon described *T. hirsti* from Queensland.
1929. Hirst stated that *T. hirsti* was probably identical with *T. pseudoakamushi* Hatori.
1930. Tanaka *et al.* described *T. autumnalis japonica*.
1932. Gater reported a Malayan species identical with both *T. hirsti* and *T. pseudoakamushi* Hatori (after Walch); he called the Malayan species *T. hirsti*. He also emphasized the difference between Walch's species and that of Kawamura and Yamaguchi. In addition, he stated that the species identified by Kitashima and Miyajima as *L. autumnalis* Shaw was definitely distinct from *T. autumnalis japonica*; that it was not *T. autumnalis* Shaw; and that it was actually very close to *T. pseudoakamushi* Hatori from Sumatra.
1939. Gunther described *T. hirsti* var. *buloloensis* (which had acquired a synonym, *T. hirsti* var. *morobensis*, nom. nud.) from New Guinea, and suggested that it was only a local variant, closely allied to *T. pseudoakamushi* Hatori.
1939. Gunther bred nymphs of *T. hirsti* var. *buloloensis*, and established their identity with *T. minor*.
1939. Womersley discounted the importance of the local variations between *T. hirsti* and *T. hirsti* var. *buloloensis*; and identified the nymph of *T. hirsti* with that of *T. hirsti* var. *buloloensis*, and with *T. minor*.

The Australian, New Guinea, Sumatran, and Malayan species need no discussion, and the evidence is sufficient in the case of the species identified as *L. autumnalis* Shaw from Formosa. There is also no doubt that Walch was correct in identifying his species with Hatori's *T. pseudoakamushi*, and therefore Hatori's species is also identical with *T. minor*.

Because Berlese's description of *T. minor* is based on an imperfect specimen, Miyajima's contention that *T. mediocris* is identical with it cannot be directly proved or disproved. There is the collateral evidence of Walch, however, on the close resemblance between the Sumatran nymphs and *T. mediocris*; and of Kawamura and Yamaguchi, who suggested that their species was the larva of *T. mediocris*. Walch and Gater both pointed out slight differences between this larva and that of Walch, while Walch noted minor differences between the nymphs. The host relationships agree, however, and the writer believes that the identification is valid.

In the writer's opinion, the following is therefore the complete list of synonyms.

TROMBICULA MINOR Berlese 1904.

T. mediocris Berlese 1912 (Java); Kawamura and Yamaguchi, 1921 (Formosa).

Non *Leptus autumnalis* Shaw 1790, according to Kitashima and Miyajima, 1918 (Formosa).

T. pseudoakamushi, Hatori 1919 (Formosa), according to Kawamura and Yamaguchi, 1921 (Formosa); according to Walch, 1923 (Sumatra).

T. pseudoakamushi var. *deliensis*, Walch, 1924 (Sumatra).

T. pseudoakamushi (var. *deliensis*?) Walch, 1925 (Sumatra).

T. hirsti Sambon 1927 (Australia), according to Gater, 1932 (Malaya).

T. hirsti var. *morobensis* (nom. nud.), Gunther, 1938.

T. hirsti var. *buloloensis* Gunther 1939 (New Guinea).

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FOUR LARVAL TROMBIDIIDAE FROM BRITISH NORTH BORNEO (ACARINA: TROMBIDIIDAE).

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

(Twelve Text-figures.)

[Read 25th September, 1940.]

These specimens were very kindly brought to me from British North Borneo by Mr. George M. Rio, of Bulolo; he obtained them from the mouse deer.

Genus Trombicula Berlese 1905.

Redia, ii, fasc. 2, 155.

Trombicula bodensis, n. sp. Figs. 1, 2, 3.

Body oval, widest at level of coxae iii. Striations fine and well-defined; pitting very strong, on scutum, maxilla, and coxae. Colour orange. L,* 285μ; W, 211μ; newly-hatched, 150 × 134μ; largest seen, 363 × 250μ. Maxillary setae short, slightly curved, with fine branches on the convex side. Chelicerae short and stout; dorsoapical tooth single, blunt; ventral tooth tiny, sharp, opposite the dorsoapical. A nude seta on each cheliceral sheath. Palpi rounded; a curved nude seta on ii; a similar seta on iii; on iv, a short nude seta near the base, a longer finer one half-way. Appendiculum very small, flattened, bearing a short stout spur and about four branched setae. Palpal claw bifurcate; the ventral element stout and straight but with a curved blunt tip; the dorsal element fine and sharp. Scutum oblong, twice as wide as long; L, 37·5μ; W, 75μ. Anterior margin smoothly concave; anterior corners angular, projecting laterally; lateral margins concave; posterior margin sinuate, slightly convex opposite the pseudostigmata; posterior corners angular, projecting laterally. Scutal setae 5, stout, with short branches on all sides. The AM back from the anterior margin, behind the AL; the lateral setae in the corners. AM, 47μ; AL, 38μ; PL, 50μ. Pseudostigmata near the posterior margin, just in front of the PL setae; 28μ apart. Pseudostigmatic organs filiform, with a few short branches on the distal third; L, 60μ. Ocular shield 3μ from scutum. Eyes double, the anterior slightly larger, set opposite the pseudostigmata; the posterior behind the PL setae. Body setae 60(64); those of the dorsum and the last row of the venter stout, with short branches on all sides; the remainder of the venter finer and shorter with fine branches on the convex side only. Dorsum, setae 30(32), in rows as follows: 2, 8, 6, 6, 6, 2(4). Venter, setae 30(32), in rows as follows: 2, 2, 10(8), 4(8), 4, 4, / 4; the anus is between rows 5 and 6. Legs relatively long: i, 180μ; ii, 125μ; iii, 200μ. Leg setae slender, slightly curved, with fine branches on the convex side. Coxal setae single. Bases of sixth segments not unduly constricted, apices not unduly expanded. Tarsi i and ii stout and blunt; tarsus iii longer and narrower. A relatively long, stout spur on tarsi i and ii; no long nude seta on iii.

Principal host; Water chevrotain, mouse deer, *planduk* (*Tragulus borneanus* Miller 1902), colonies on legs, Bode River, near Sandakan, British North Borneo, August, 1939.

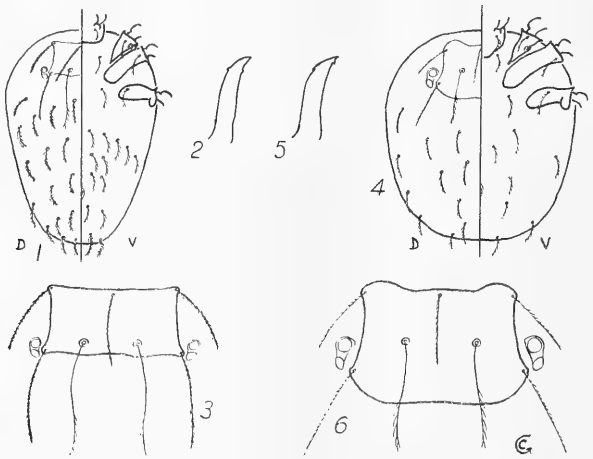
Type specimen at the School of Public Health and Tropical Medicine, University of Sydney.

* As in previous papers, AL = anterolateral, AM = anteromedian, PL = posterolateral, L = length, W = width.

TROMBICULA WICHMANNI Oudemans 1905. Figs. 4, 5, 6.

Entomol. Bericht., i, No. 22, 217.

On the same host were several colonies of another *Trombicula* which corresponds almost exactly with Oudemans' description of *T. wichmanni*. This description is a very careful and complete one, but unfortunately few measurements are given, and the old style of naming the segments of the appendages is followed. The old nomenclature is cumbersome and confusing; a numerical system is to be preferred. After much hesitation, and with considerable diffidence, the writer has decided to offer the following supplementary description, based on his own specimens, for the purpose of bringing it into line with recent work; and to incorporate certain measurements, particularly of the scutum, by the aid of which quicker and easier comparison of species can be made possible. It has been thought desirable to give a complete description rather than to set out mere supplementary notes, since those alone would be useless without the original paper to refer to.



Figs. 1-3.—*Trombicula bodensis*, n. sp. 1, Composite dorsal and ventral diagram. 2, Chelicera. 3, Scutum.

Figs. 4-6.—*Trombicula wichmanni* Oudemans 1905. 5, Chelicera. 6, Scutum.

Body a blunt oval, flattened posteriorly in newly-hatched larvae, bluntly rounded in older ones. Widest just behind coxae iii. Striations fine and weak, especially on the venter and the posterior portion of the dorsum. Pitting strong on the scutum, but very fine, arranged along fine striations, on the maxilla and coxae. Colour orange. L, 297μ; W, 232μ; newly-hatched, 168 × 150μ; largest seen, 416 × 292μ. Maxillary setae fine, curved, with long branches on the convex side. Chelicerae short, stout, curved; dorso-apical tooth single, small, blunt; ventral tooth nearer the apex, sharp and squared. A fine nude seta on each cheliceral sheath. Palpi angular; a stout seta with a few branches on ii; a nude seta on iii; on iv, two nude setae and one branched seta. Appendiculum rounded, bearing a short spur at the base, one nude and four branched setae towards the apex. Palpal claw bifurcate, the elements almost equal, stout, sharp, curved. Scutum rounded, concave before and convex behind, half as wide again as long; L, 64μ; W, 95μ. Anterior margin strongly convex in the lateral fourths, concave and sinuate in the middle; anterior corners slightly angular, at the junction of the lateral and anterior margins; lateral margins slightly concave; posterior margin strongly convex, the middle three-fifths straight, the lateral fifths curving forward; posterior corners angular and projecting. Scutal setae 5, almost straight, slender, with short fine branches on the convex side; the AM in line with the AL; the lateral setae in the corners. AM, 36μ; AL, 38μ; PL, 54μ. Pseudostigmata half-way back, 37·5μ apart. Pseudostigmatic organs filiform, fine, with six long branches on the distal half; L, 56·3μ. Ocular shield 5μ from the scutum (further in fully-engorged specimens). Eyes double,

the anterior the larger, set opposite the pseudostigmata; the posterior opposite the PL setae. Body setae 40: those of the dorsum stout, with very fine short branches on the convex side; those of the venter finer and shorter, with relatively longer branches. Dorsum, setae 22, arranged in rows as follows: 2, 6, 6, 4, 2, 2; row 6 is on the posterior margin of the body. Venter, setae 18, in rows as follows: 2, 2, 4(2), 2(4), 2, 4, 2; in older specimens rows 3 and 4 merge into one; the anus lies between rows 5 and 6; row 7 is on the posterior margin of the body. Legs relatively long: i, 225μ; ii, 210μ; iii, 240μ. Leg setae fine, long, curved, with fine branches on the convex side. Coxal setae single. Bases of sixth segments all constricted, apices expanded. A short nude seta on the apex of the sixth segments of legs i and ii. Tarsi long and slender, that of leg iii very much so. A blunt spur and a sharp spur on tarsus i; a sharp spur on tarsus ii; a long fine straight nude seta on tarsus iii.

Principal hosts: Goura pigeon (*Goura scheepmakeri* Finsch 1875), colonies on the head, Tawarin and Jamür, Dutch New Guinea, 1903; water chevrotain, mouse deer, *planduk* (*Tragulus borneanus* Miller 1902), colonies on the legs, Bode River, British North Borneo, August, 1939. Casual host: Man, North Celebes, 1903.

Genus Gahrliepia Oudemans 1912.

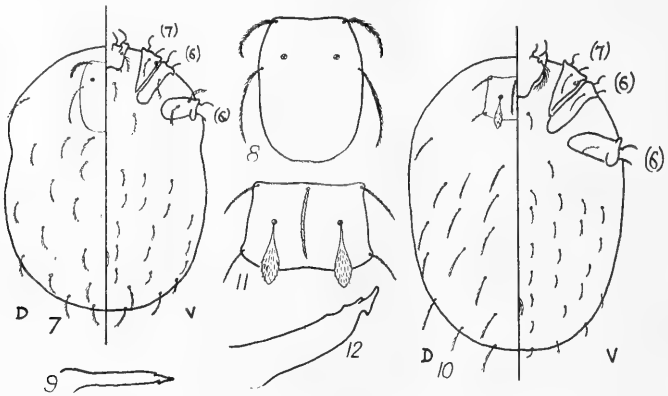
Ent. Ber. Nederl. Ver., iii, No. 67, 273.—*Typhlothrombium*, Oudemans, ibid., iii, No. 56, 1910, 105.—*Schöngastiella*, Hirst, *Bull. Ent. Res.*, vi, 1915, 188.

Gater in 1932 discussed this genus, and stated that ". . . the number of scutal setae is not a sound criterion for the separation of genera in this group". He placed six new Malayan species in the genus, in spite of the fact that they had, respectively, 7 to 10, 7, 6, 4, 2, and 2 pairs of scutal setae; that in all six the palpal claws were trifurcate; and that four had two eyes on each side and two had none. (The classical description of the genus, based on a single species, *G. nanus*, specifies only one eye on each side, 5 pairs of scutal setae—3 pairs in *Schöngastiella*—and the palpal claw bifurcate.) There is the objection that, since their pseudostigmatic organs are missing, the placing of *G. ciliata*, *G. rutila*, and *G. turmalis* in this genus must be regarded as provisional only. Nevertheless, the other three are certainly correctly placed. It follows, therefore, that Gater's decision to re-include Hirst's *Schöngastiella* within the same genus, for similar reasons, is a good one also. The expanded conception of *Gahrliepia* would preferably be on the following lines: Larva with one dorsal median scutum; scutum large and tongue-shaped, much longer than broad; anterior portion occupied by the pseudostigmatic organs and two pairs of true scutal setae; posterior portion strongly salient, bearing a variable number of paired accessory scutal setae; pseudostigmatic organs capitate.

Gahrliepia rioi, n. sp. Figs. 7, 8, 9.

Body a broad rounded oval, widest at level of coxae iii, with a sharp, shallow constriction at each side two-fifths of the distance back. Striations coarse and moderately strong. Weak pitting on scutum, maxilla, and coxae. Colour orange. Only moderately engorged specimens were taken: L, 277μ; W, 204μ; largest seen, 292 × 223μ. Maxillary setae long, curved, with a few long branches on the convex side. Chelicerae short, straight, sharply pointed; dorsoapical tooth single, a small sharp barb; ventral tooth a rounded swelling only, proximal to the dorsoapical. A long slender nude seta on each cheliceral sheath. Palpi angular; a long curved seta with branches on the convex side on ii; a long nude seta on iii; on iv, a short, stout, nude seta near the base, a short branched seta half-way, and a similar seta near the apex. Appendiculum small, rounded, bearing 3 nude setae and 4 branched setae. Palpal claw trifurcate, the middle and dorsal elements straight with hooked points, the ventral shorter and finer. Scutum tongue-shaped; L, 75μ; W, 55μ. Anterior margin straight or very slightly concave; anterior corners rounded; lateral margins slightly convex; posterior margin strongly salient; posterior corners almost straight. Scutal setae 4: the AL short, stout, curved, with long branches on all sides, set in the anterior corners; the PL longer, less curved, with branches on the convex side only, set in the posterior corners. AL, 28μ; PL, 40μ. There are no accessory scutal setae. Pseudostigmata one-third of the distance back, in front

of the PL setae; 28μ apart. Pseudostigmatic organs missing from all specimens. No eyes. Body setae 72(66 to 74): those of the dorsum and the last two rows of the venter long, stout, curved, with branches on the convex side; the remainder of the venter shorter and finer. Dorsum, setae 30, in rows as follows: 2, 6, 6, 6, 4, 4, 2. Venter, setae 42(36 to 44), in rows as follows: 2, 2, 6(0 to 8), 8(6), 6, 6, 6, / 4, 2; rows 3 and 4 are



Figs. 7-9.—*Gahrliepia rioi*, n. sp. 8, Scutum. 9, Chelicera.
Figs. 10-12.—*Neoschöngastia bodensis*, n. sp. 11, Scutum. 12, Chelicera.

irregular, the former sometimes being absent; the anus lies between rows 6 and 7; row 9 is on the posterior margin of the body. Only six segments in legs ii and iii; i, 135μ; ii, 110μ; iii, 140μ. Leg setae short, stout, curved, sharply tapering, with a few stout branches on the convex side. A single seta on coxae i and ii; two setae on coxae iii. Penultimate segments not unduly constricted or expanded; tarsi all short and blunt. A short, stout, blunt spur on tarsus i; that on ii finer and sharper; neither spur nor nude seta on iii.

Casual host: Water chevrotain, mouse deer, *planduk* (*Tragulus borneanus* Miller 1902). Bode River, British North Borneo, September, 1939; ten specimens embedded in the legs.

Type specimen at the School of Public Health and Tropical Medicine, University of Sydney.

Genus Neoschöngastia Ewing 1929.

Manual External Parasites, 187.

Neoschöngastia bodensis, n. sp. Figs. 10, 11, 12.

Body a broad oval, widest at level of coxae iii. Striations coarse and moderately strong. Pitting on scutum, maxilla, and coxae. Colour orange. L, 308μ; W, 225μ; only partly engorged specimens taken. Maxillary setae long and curved, with very long branches on the convex side. Chelicerae stout, tapering abruptly; the dorsoapical tooth single, small and sharp; a row of three blunt teeth along the distal third of the ventral surface—these ventral teeth are very small and indistinct in most specimens; they are in no respect comparable to the long row of closely-set dorsal teeth of the genus *Schöngastia*. A long slender nude seta on each cheliceral sheath. Palpi rounded, a short nude seta on ii; a long fine seta with one fine branch half-way down, on iii; on iv, one long branched seta. Appendiculum small, rounded, bearing 2 short stout nude setae and 4 very long stout branched setae. Palpal claw trifurcate, the middle element very stout, curved, and blunt; the dorsal element shorter, the ventral the shortest. Scutum oblong; L, 47μ; W, 70μ. Anterior margin sinuate; anterior corners angular; lateral margins slightly concave; posterior margin convex, concave in the middle third; posterior corners angular. Scutal setae 5; the AM set back from the anterior margin, behind the AL, stout, with short branches; the lateral setae in the corners, shorter and finer. AM, 37·5μ; AL, 25μ; PL, 20μ. Pseudostigmata half-way back, 34μ apart. Pseudostigmatic

organs capitate, leaf-shaped, covered with long straight setules; L, 33μ; head, 20·5 × 11μ; stem, 12·5μ. Crest represented by short faint curved lines set obliquely in front of and behind the pseudostigmata, the posterior ones very indistinct. Ocular shield faint, 13μ to 19μ from scutum. Eyes double, the anterior the larger, opposite the pseudostigmata; the posterior very faint, opposite the PL setae. Body setae 76(80); those of the dorsum short, stout, with short branches on the convex side; those of the venter similar, but very short and fine. Dorsum, setae 30, in rows as follows: 2, 6, 6, 6, 4, 4, 2; row 7 is on the posterior margin of the body. Venter, setae 46(50), in rows as follows: 2, 2, 8(10), 8(10), 6(8), 8(6), 6, 4, 2. Legs long; only 6 segments in ii and iii; i, 146μ; ii, 118μ; iii, 167μ. Leg setae long, fine, with short branches on the convex side. Coxal setae single. Penultimate segments neither constricted nor expanded; all tarsi short and blunt. A long stout sharp spur on tarsus i; a shorter one on ii; neither spur nor nude seta on iii.

Principal host: Water chevrotain, mouse deer, *planduk* (*Tragulus borneanus* Miller 1902), colonies on legs, Bode River, British North Borneo, September, 1939.

Type specimen at the School of Public Health and Tropical Medicine, University of Sydney.

Neither the multiple ventral teeth nor the missing segments in the mid- and hind-legs appeal to the writer as of sufficient importance to warrant erecting a new genus. The latter condition is analogous to that found in *N. impar* and *S. oudemansi*.

Acknowledgements.

My thanks are due to Mr. G. M. Rio, who spent part of his holiday collecting specimens for me; to Mr. E. Le G. Troughton and Mr. T. Iredale, who identified hosts for me; and to Mr. F. H. Taylor, who checked this paper for me.

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MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. VII.

ON BODY-COLOUR; AND ON SPECIES OF TABANIDAE, CYRTIDAE AND ASILOIDEA.

By G. H. Hardy.

[Read 30th October, 1940.]

A theory of body coloration.—Williston (1908, 43–5), discussing the vestiture found on flies, concludes: ". . . the tomentum can only correctly be used as the designation for flattened, scale-like or stubble-like, more or less recumbent hairs, which gradually merge into dust or pollen, which is so generally represented in Diptera, and upon which the determination of many species must largely depend."

This expression is responsible for clouding the issue concerning the gradual change of the vestiture from pubescence, to tomentum, to dust (herein called the pulverulent overlay), all being regarded as having a common basis. Actually I have found no point where pubescence, tomentum and the like, ever merge into the pulverulent overlay, and so conclude they have had different origins. To give a more satisfactory account of this is the purpose of the present note.

The new theory has, of course, to be based on the view that the pulverulent overlay arises directly from the surface of the cuticle and is actually part of the cuticle that has crumbled into dust instead of being in homogeneous continuity with the body wall. It is a superlayer that has developed, perhaps, from an extra development of the normal cuticle.

It is also necessary to note that, when arranged phylogenetically, some large genera show that there is a gradual merging from the normal pigmented and somewhat shining cuticle to a highly polished one, and even to iridescence, and it is upon this bare surface that first comes a slight covering that is the beginning of a pulverulent overlay. The thin transparent layer that forms the polished surface and the powdery covering both show white in the primitive state, both being without pigmentation; in transition from one to the other, it appears as if the glass-like surface crumbles to a white powder just as transparent glass would crumble to white.

It is assumed that an unpigmented layer which gives the high polish is superimposed on the normal pigmented part of the cuticle and in continuity with it. Then it is assumed that this unpigmented layer breaks down into a pulverulent overlay. It must be noted that the overlay might be developed by the failure of the layer to form a homogeneous unit with the cuticle and thus be derived directly from the body-wall. It is not yet determined which of these actually takes place—both may do so.

Development of the coloration in the cuticle depends upon the supply of materials from waste products, and there seems to be a very definite limit to coloration found in the body-wall, ranging from yellow, which is the primitive coloration, through red, green and blue, each colour separately or in combination. A red-green gives copper, and a red-blue gives purple, but there are limits to shades developed this way. The process goes on by a deepening of these pigments in the cuticle until black, the ultimate, is reached.

It is the pulverulent overlay that shows the wider development in colours and tones. the reason being obvious when one accepts the view that the overlay is developed from the surface of the cuticle. As already stated, the clear glass-like surface layer of the cuticle breaks up into a silvery-white, but if the layer be impregnated with a yellow-red pigment, then the overlay is golden, and a black pigment there would give an ashy-white. The vast array of powdery browns met with doubtless is due to mixed pigments containing red.

Comparisons made between many of these tones in the pulverulent overlay and the colour of the cuticle lying below, suggest that the views discussed are justified, so that there may be a very definite relationship between colorations as seen in the evolutionary stages of development, yellow being the most primitive pigment colour noted.

Actually these ideas arise from a close study of coloration in the Muscoidea, making it advisable to introduce certain of the genera into these notes, but the system is now being adopted for colour studies in the lower Brachycera, where the tracing of the system is not quite so obvious.

In Muscoidea, the genus *Amenia* is the most primitive of the Tachinid flies, so much so that Townsend grades it as being a member of the Calliphoridae under his artificial classification. It has all the structures of the Tachininae, with certain features of coloration that occur in common with the Dexiinae, with which it has frequently been confused. The genus retains the primitive yellow head, but the rest of the body is largely blue-green and highly polished. The polished part also has some, but very limited, silvery powdered overlay, mainly in the form of spots below which the ground colour is darker and certainly less polished.

The white pulverulent overlay is a characteristic feature of *Microtropeza*, the primitive genus of the second section in the Tachininae. In this genus there is a wider variation in colour, but there is a strong tendency to retain the yellow head. Moreover, the reddish-yellow abdomen, as well as the more normal metallic-blue, is represented in the genus. Certain forms of metallic Dexiinae also tend to retain the yellow head, thus connecting the three chief groups of Tachinid flies in a striking manner.

There is the same story represented in the Calliphoridae, for here the occurrence of yellow species conforms to phylogeny worked out on structural development. Moreover, certain genera of the Tachinidae show the parallel colour development seen within the genus *Calliphora*, and the yellow in the body colour seems to be primitive to all such groups, while white remains the primitive coloration for the pulverulent overlay. This permits certain genera to be arranged on a coloration basis, when the species are widely different in body colours and in overlay colours.

Tabanidae.

Colour scheme.—A wide range in coloration and general appearance occurs in this family, and has been responsible for a diversity of opinions concerning generic limits. It is now generally conceded that in Australia there are only a few valid genera, several with numerous species. *Silvius*, in accordance with those species known to me, is comparatively bare in comparison with *Tabanus*, which usually has a conspicuous amount of the pulverulent overlay even when tomentum is plentiful, and the case is similar in *Scaptia*. *Pelecorrhynchus*, which is regarded as being rather primitive, exhibits a variety of coloration that emphasizes the evolutionary aspect in development and coloration of its pulverulent overlay.

In *Scaptia* there are rather shining yellow bare species like *S. concolor* Walker and *S. inflata* Walker, and the darker, more hairy *S. constans* Walker, all of which may prove to be more primitive than the metallic *S. violacea* Macq. On the other hand, the yellow species in *Tabanus* belong to the *avidus*-group which is highly specialized and probably an offshoot from a lowly organized *Tabanus* type. The more usual form of the genus has only one species regarded as somewhat primitive, namely *T. cyaneus* Wiedemann, which is bare and metallic blue.

Pelecorrhynchus, as shown by me (1933, 412), has three groups, each conforming to its colour-scheme and there is no overlapping in this respect. The *fusconiger*-group has the abdomen bare and slightly shining, black varying to deep red-black, and the pulverulent overlay is limited to the thorax. The *personatus*-group has developed the whitish overlay on both thorax and abdomen; on the thorax of two species, lines of orange-yellow have developed.

The orange coloration is consistent on the thorax of the *fulvus*-group, and also on the abdomen of the female, but on the male the abdomen conforms to those of the other two groups, as indicated in the key to species given below. Thus in coloration

the *fusconiger*-group is the lowest and the *fulvus*-group the most advanced type within the genus.

Key to the Pelecorrhynchus fulvus-*group.*

1. Thorax above broadly orange with a central stripe of deeper tone; black laterally. Male abdomen shining black. Wings orange with an apical black blotch ..... *fulvus* Ricardo
   Thorax above with a pair of yellowish stripes, otherwise black 2
2. Wings with a dark central spot on costa, another towards apex, and a small one between them remote from costa. Male abdomen with broadly interrupted white bands, which are thus reduced to two spots on each segment ..... *mirabilis* Taylor
   Wings with a dark broad mark along costa, reaching beyond centre, and a dark subapical blotch. Male abdomen entirely black and shining ..... *distinctus* Taylor

In the absence of the female, there is a liability to confusion in distinguishing these species from *P. deuqueti* Hardy and *P. flavipennis* Ferguson, both of which have five or more black marks on the orange wing and belong to the *fusconiger*-group. The male of *P. mirabilis* is distinguished from the *personatus*-group by its very small size and the three dark spots on the wing instead of at least five or none.

PELECORRHYNCHUS OLIVEI Hardy.

PROC. LINN. SOC. N.S.W., lviii, 1933, p. 413.

♀. Similar characters to those of the male; eyes widely separated.

Omitted from the original description, the above is needed to establish the allotype and paratype females which are before me.

CYRTIDAE.

ONCODES BASILIS Walker.

Walker, *Ins. Saund. Dipt.*, 1852, 203; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 78 (which see for synonymy and references given there); Brunetti, *Ann. Mag. Nat. Hist.*, (9) xviii, 1926, 599.—*O. insignis* Brunetti, ibid., 601.—*O. fratellus* Brunetti, ibid., 604.—*O. castaneus* Brunetti, ibid., 605.—*O. victoriensis* Brunetti, ibid., 605.

Synonymy.—I am indebted to Dr. B. M. Hobby, and Mr. H. Oldroyd, who have, at my request, brought together and made comparisons between the types of Westwood in the Hope Museum, Oxford, and those of Walker and Brunetti in the British Museum. The kind permission of Professor G. D. H. Carpenter enabled this to be done. The ten types are still in existence, that of *O. flavescens* White, in the British Museum, being "very badly broken" (Oldroyd); *O. nigrinervis* White, still in excellent order, is before me, and the other two types of White are in the Littler Collection at the South Australian Museum.

Of the types in England, Mr. Oldroyd writes: "It seems very probable that one species might be sufficiently variable to include all of them, though *variegatus* Brun. has a distinct thoracic pattern of which there is no trace on the others." The sketch supplied shows a colour variation not otherwise known to me, so we both agree to its retention as a separate species.

Walker's type was compared by him with a Ceylon species, not with the Australian material of which it forms a part, except in so far as he included it in his key. The key itself is obscure, containing "conspicuously characteristic species" for *variegatus* and *insignis*, the rest being "less characteristic"; his distinguishing characters break down in other respects.

For the purpose of handling varieties in colour characters, the only feature upon which the segregations rest, I have drawn up the following:

Key to species and varieties of Oncodes.

1. Thorax entirely black above, at most a little brownish at the humeral and post-alar calli ..... *basilis* Walker. 2
   Thorax broadly brown at sides, otherwise colour characters conform best to the description of *castaneus*, except that the posterior legs are mainly black ..... *variegatus* Brunetti

O. basilis colour varieties.

2. Abdomen well marked with yellowish-brown; usually black lateral spots, and a central area frequently limited to one or more black spots, the rest brown. Femora half black on

typical form, varying to mainly black (*tasmanica*) and to mainly yellow (*flavescens*). ..... *basilis* Walker; *darwini* Westw.; *tasmanica* Westw.; *flavescens* White; *insignis* Brun.; *castaneus* Brun.

The yellowish-brown of the abdomen limited to a subapical band. Femora and tibiae mainly yellow; except on *ater* the femora are black .... *fortumni* Westw.; *ignava* Westw.; *ater* White; *fraternum* Brun.

No brown whatever on abdomen* 3

3. Males† ..... none hitherto described

Females. Femora and tibia black or mainly so, varying to brown .... *nigriventris* White; *pygmaeus* White; *victoriensis* Brun.

The characters so grade, one to the other, that I have been unable to place any of the series seen by me into more than a single species; though there are no structural characters that may aid, I feel convinced that there is a complex of species before me.

After the appearance of Brunetti's paper, Dr. I. M. Mackerras made slides of terminalia (some of which I have seen), attempting to establish specific identities in this manner, but although he took forms that appeared to be distinct, he found no differences. I have since given attention to this matter, and think that some of my material, but not likely any of the types, may show differences in the male terminalia, but the matter will have to wait for fresh material to be studied.

Recently I have added to my collection a series of specimens showing wide colour variations, all taken from a single tree in my garden at Sunnybank, and none of the males showed any differences in the terminalia. The tree itself is frequented by these flies over the autumn months every year, as also is the ground for some yards away from the tree. I seldom see these flies elsewhere in Sunnybank.

Apioceridae.

Genus Apiocera Westwood.

Lond. Edin. Phil. Mag., vi, 1835, 449—type *A. fuscicollis* Westw. = *asilica* Westw.—*Tapinocera* Macquart, *Dipt. Exot.*, suppl. 1, (2) 1838, 78—type *Laphria brevicornis* Wied.—*Pomacera* Macquart, ibid., suppl. 2, 1847, 49—type *P. bigotii* Macq. = *asilica* Westw.

Synonymy.—The synonymy given above is not new, but the identities of the types are now ascertained. For the elucidation of this matter I am indebted to Dr. B. M. Hobby and to Mr. H. Oldroyd, who have made comparisons between those specimens in the Hope Collection and those in the British Museum. Mr. K. R. Norris has supplied me with specimens of *A. pallida* Norris, paratypes, which species, as he states, is not related to *A. maritima* Hardy; nevertheless, I note that the frons on the female is almost parallel sided, standing between the strongly converging frons and that normal diverging frons which seems to be a standing character for the male and all other species of *Apiocera* known, as well as those of the genus *Neorhaphimoides*, specimens of which were also received from Mr. Norris.

Before me are specimens of *A. pica* Norris (Perth, 16th November, 1912; 2 ♂, 2 ♀) which are related to *A. asilica* Westw.; judging from description, *A. tonnoiri* Norris is related to *A. imminuta*, n. sp., which I have previously (Hardy, 1933, p. 418) referred to as a coastal sand-dune species. These two cases are the closest contacts I have yet detected between the *Apiocera* species of the western and the eastern regions of Australia.

Terminalia.—On the male, the dorsal lamella is divided, the ventral lamella present, contiguous with the aedeagus and hence there is no median plate. The aedeagus is very short and has a small armature. The ninth tergite is developed to forceps; the lower forceps are developed and the claspers are hinged, frequently having strong black bristles. The ventral plate is narrow, blunt apically.

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* In all living specimens there is a line-like apical margin that is white, and liable to turn yellow after death; this is not to be confused with the subapical and adjacent brown nearly always present on males.

† According to description, *O. ater* White was based on the male having the hind margin of the abdomen narrowly and indistinctly brown, but Dr. Hobby refers, in a letter, to one on which it is all black, so evidently a second specimen was identified by White at a later date and would fall to this position, agreeing with several other specimens before me.

In life the eyes are red, with a slight tinge of green reflection, and the proboscis is able to be retracted and protruded for the length of the labellum.

Key to species of Apiocera *in the eastern States.*

1. Brick-red species (not seen) ..... *vulpes* Hermann
   Black or brown species 2
2. Eye-summit-eye proportion on male 2 : 4 : 2 (summit 50% of total head-width); on female 5 : 14 : 5 (58%). Frons strongly converging from summit towards antennae. Colour markings absent, the ground colour being obscured completely by a whitish pulverulent overlay, or, if markings are detected, they show as narrow light apical margins on the abdominal segments. Coastal sand-dunes ..... *maritima* Hardy
   Summit much narrower, less than 40% of total head-width. Frons broadening from summit towards antennae 3
3. Eye-summit-eye proportion on male 3 : 1 : 3 (14%), and on female 11 : 10 : 11 (31%). A broad central stripe of brown on the thorax is entirely without a median white line, and the whole insect is of chocolate-brown colour with markings otherwise not unlike those of *asilica*. Antennae and proboscis reach about the same distance, and the palpi reach to the labellum ..... *immedia*, n. sp.
   Thorax with a median white line, making four dark and five whitish stripes 4
4. Eye-summit-eye proportion on male 11 : 6 : 11 (21%), on female 5 : 6 : 5 (37%). Thorax with the lateral dark stripe divided into three spots well rounded on front edge; the proboscis is short and the palpi reach the labellum ..... *asilica* Westwood
   Thorax with the lateral stripe practically complete, divided by a very thin white line that is straight and not particularly noticeable 5
5. Eye-summit-eye proportions on male 9 : 4 : 9 (18%), on female 8 : 7 : 8 (30%). Abdominal markings reduced to a pair of white spots on each segment .... *brevicornis* Wiedemann
   Eye-summit-eye proportion on male 7 : 5 : 7 (26%), on female 5 : 4 : 5 (28%). Abdomen with a pair of white stripes complete or practically so. The palpi fail to reach the labellum of the long proboscis by nearly the length of the second segment ..... sp.
   Abdominal markings reduced to white along the posterior margin of the segments 6
6. Eye-summit-eye proportions on male 7 : 5 : 7 (26%), female unknown. Antennae placed very low on head and the proboscis and palpi are unusually short. Coastal sand dunes ..... *imminuta*, n. sp.
   Eye-summit-eye proportions on male 3 : 2 : 3 (25%), on female 5 : 6 : 5 (37%). Palpi fail to reach the labellum of the long proboscis by about the length of the second segment. Western plains ..... *norrisi*, n. sp.

Apiocera maritima Hardy.

Proc. Linn. Soc. N.S.W., lviii, 1933, 416, fig. 1.

No bristles have been detected on the claspers of this species.

Hab.—Queensland and New South Wales. Miss K. English has submitted specimens from the latter State for identification.

Apiocera immedia, n. sp.

Apiocera sp., Hardy, Proc. Linn. Soc. N.S.W., xlvi, 1921, 296, fig. 16.

This very distinctive species is readily distinguished by the characters given in the key. It is of a deep shining chocolate-brown colour and without the white median thoracic line recorded on *A. vulpes* Herm. and occurring on all the others given below. A pair of slender white stripes reaches the transverse suture, and may be traceable to a pair of white spots placed just before the apical margin. Laterally another pair of white stripes reaches the transverse suture, slightly interrupted at the margin of the humeral callus, followed by two pairs of white spots, one above the wing insertions, the other on the postalar callus, reaching the scutellum which is without visible marks. On the male the abdomen has a pair of white spots, overlapping insertions, at the apex of the third to sixth segments; on the female similarly marked on the first to fourth segments. Head, pleura and venter normal, as on *A. asilica*. This is the only species I have seen that has a tendency for the whitish markings to become yellow, as against the ashy-white colouring of the others. Length 24–26 mm.

Hab.—N.S.W.: Sydney, 1 ♂, 2 ♀, 26th December 1918; probably from La Perouse.

Apiocera asilica Westwood.

Lond. Edin. Phil. Mag., vi, 1835, 449; *Isis*, ii, 1838, 87; *Arcana Entom.*, i, 1841, 56; Walker, *List Dipt. B. Mus.*, vi, suppl. 2, 1854, 56; Osten-Sacken, *Berl. Ent. Zeit.*, xxvii, 1883, 294.—*A. fuscicollis* Westwood, ibid., 1835, 449; ibid., 1838, 87; ibid., 1841, 56;

Hermann, *Deut. Ent. Zeit.*, ii, 1909, 107.—*A. moerens* Westwood, *Arcana Entom.*, i, 1841, 56, Pl. 14, fig. 6; Walker, *List Dipt. B. Mus.*, i, 1848, 229; Hansen, *Fabrica oris Dipt.*, 1883, 170, Pl. 5, figs. 22–28; Hermann, *Deut. Ent. Zeit.*, ii, 1909, 107.—*Pomacera bigotii* Macquart, *Dipt. Exot.*, suppl. 2, 1847, 49, Pl. 2, fig. 1; Hermann, ibid., 1909, 107.

Synonymy.—A letter from Dr. B. M. Hobby (which includes the view also accepted by Mr. H. Oldroyd) states that the types of the two first species of Westwood are in the Hope Museum, both recognized as being the types in Sir Edward Poulton's handwriting. The type of *A. moerens* is apparently lost and so specimens regarded as conspecific were used for comparison. The two types have lost nearly all their pulverulent overlay and are more or less uniform dull-black; only a remnant of the abdomen remains in *fuscicollis*. Size, shape, antennae and mouthparts, and faint tracings of markings follow closely those of *moerens*, so it is advisable to regard all three as belonging to one valid species. The only difference detected is in the lighter wing-veins on *fuscicollis*.

Hermann regarded *A. fuscicollis* and *A. moerens* as being two species, and *A. bigotii* as a possible third, but it is doubtful if he could have had any correctly named specimens; his references are included above, but he gave no descriptions enabling his species to be identified. It seems to me probable that Macquart's species was from Sydney, as the family is quite unknown from Tasmania, and Macquart's figure agrees with the present interpretation, except that the anterior half of the thorax has no proper marking, and perhaps was greasy. Williston (1908, fig. 70) gives a very good figure of the male without a specific name.

Hab.—Queensland, New South Wales and Victoria. Specimens from all these States are before me; the distribution of the species extends from the coast to the Mallee districts (Ouyen) of Victoria. The claspers were found to correspond rather well with those of *A. pica* Norris, which species has the markings rather similar.

Apiocera brevicornis Wiedemann.

Laphria brevicornis Wiedemann, *Auss. zweifl. Ins.*, ii, 1830, 646.—*Tapinocera brevicornis* Macquart, *Dipt. Exot.*, 1, ii, 1838, 79, Pl. 6, fig. 15; Walker, *List Dipt. B. Mus.*, vii, suppl. 3, 1855, 573; Schiner, *Verh. Zool. Bot. Ges. Wien*, xvi, 1866, 649.—*Apiocera brevicornis* Osten-Sacken, *Berl. Ent. Zeit.*, xxvii, 1885, 294.

As this species is said to be rather slim and has yellowish hairs on the frons, it cannot be identical with *asilica* Westw., so I attach the name to a common species that best fits the description. The claspers, with few bristles, are not unlike those of *A. minor* Norris.

Hab.—New South Wales; the specimens before me are all from the Blue Mountains, where it is common, 3 ♂, 5 ♀, January 1926.

Apiocera sp.

I leave unnamed a Queensland species that is quite distinctive. Two Brisbane females are before me, from Sunnybank, whilst males are in Mr. F. A. Perkins' collection from Inglewood. I am uncertain if I have the sexes allied correctly.

Apiocera imminuta, n. sp.

A. sp. Hardy, Proc. Linn. Soc. N.S.W., xlvi, 1921, 296, fig. 14.

This coastal sand-dune species is known to me only from the male, and the characters given in the key are ample for the recognition of this sex. It will be noted that the summit width corresponds to that of the unnamed species, but the head is relatively much wider. The proboscis is so short that the antennae extend well beyond it, more so than shown in the figure which was drawn in perspective, and in which the antennae were placed too high, for they correspond to those of *A. tonnoiri* Norris. The median thoracic stripe is short, but the two adjacent pairs may extend unbroken to the scutellum. The apical margins of all abdominal segments are thinly bordered with white, interrupted on the three basal segments at the median line, and the lateral white stripes may extend over the four basal segments and be traceable on

others. The claspers have a dense mass of bristles almost reaching the apex. Length 15 to 18 mm.

Hab.—Queensland: Southport, 3 ♂, December 1931, one selected for the holotype. New South Wales: Sydney, 1 ♂, 1st December 1918 (probably from La Perouse), and two others, 19th January 1919.

Apiocera norrisi, n. sp.

The markings are as on *A. imminuta*, the head is normal and the proboscis is slightly longer than twice the head length, extending well beyond the antennae. The characters given in the key are ample for recognition of the species and, in addition, the wing has the first and second median veins weakened and white but complete, whereas the third and fourth median veins meet as usual, but do not continue, so the united part which normally runs to the wing margin is absent. Length, 12 to 13 mm.

Hab.—Queensland: Mungindi, 1 ♂, 3 ♀, all found resting on twigs at sundown, six miles north, along the Dareel road on red soil country. The species looked very much like an *Anabarrhynchus* (Therevidae) for which it was mistaken when seen in flight, earlier in the day, over the adjacent paddock infested with *Bassia Birchii* (Chenopodiaceae).

Named as a tribute to Mr. Kenneth R. Norris, whose work (1936) on the Apioceridae of Western Australia has formed a basis for these notes.

Asilidae.

Colour scheme.—Certain sections in this family are remarkable for their dense hairy nature, the hairs carrying colours that are excluded from this account which refers only to the cuticle colour and the pulverulent overlay. Sufficient has been worked out in a series of papers (Hardy, 1934–5) to show probable relationships between genera; when arranged in accordance with this, the coloration in the family becomes enlightening.

It is proposed here to discuss *Apiocera* with the Asilidae, the genera being arranged in accordance with the form taken by the female terminalia which gives the main guide to phylogeny.

The Phellini show that originally the ninth tergite on the female was complete and without any indication of acanthophorites. This condition presumably preceded that of *Apiocera* where a ridge is formed along the dorsal line of the ninth tergite which carries spines that turn this tergite into acanthophorites fused together. *Apiocera* also has an adaptation of its median plate that permits the protrusion of the proctiger, a feature that is found also in Brachyrrhopalini where the ridge is absent and the acathophorites are separated. Other primitive genera of the Dasypogoninae have the median plate otherwise formed, allowing of no retraction of the acanthophorites and, when present, the ridge is separated from the acanthophorites, lying between them, looking almost like an extra spine inserted there. In the more advanced genera this ridge disappears and at a later stage the acanthophorites themselves tend to atrophy and ultimately to disappear, as in most genera of the Asilinae.

Coloration is parallel to this, for the primitive *Phellus* is without a pulverulent overlay and is highly metallic in body-colour; the yellow colouring is in the hairs. It has reached the metallic-blue stage only. In *Apiocera* the body-colour on one species is said to be brick-red; the genus certainly varies from brown to black, a metallic stage being absent. The pulverulent overlay is strongly ashy-white, rarely tending towards yellow, but the genus forms a side issue carrying its own peculiar features. In the Brachyrrhopalini, yellow, red, and black predominate in the colour pattern of the body which is normally without a marked pulverulent overlay, but one species with a red thorax has a slight pulverulent overlay there and another has a distinct pattern. Most species have a slight overlay around the face and on coxae, and this may even become yellowish.

The more generalized types of the other Dasypogonini have very little overlay, but this becomes well developed in certain genera, *Chrysopogon*, *Bathypogon* and *Metalaphria* being examples, and even certain tribes, the Stichopogonini being one. The overlay is much less marked in the Atomosiini, whilst in the Laphriini the exotic species I have

examined are without the overlay, yet, amid the Australian ones, the overlay is scanty and best developed on *Laphria tectamus* Walker, the thorax having quite a distinct pattern. Otherwise the majority of forms have reached the highly metallic stage, and although Bromley (Abst. Doctor's Dissert., No. 14, Ohio Univ., 1934, 125) regards them as being "the most recently evolved of the Asilidae", this does not apply to the colour characters.* It is in the other subfamily, the Asilinae, that the pulverulent overlay is general and well developed.

The following notes, mainly on terminalia, are additional to descriptions in my 1934–5 papers.

LAPHRIA TECTAMUS Walker.

List Dipt. Brit. Mus., ii, 1849, 374.

On the male the dorsal lamella is divided, and the ventral lamella extends well beyond the dorsal one. The proctiger is fixed well beyond the undivided ninth tergite which is thus not incised. The claspers are hinged and the lower forceps are small, but the support of the two claspers seems to be in one unit supporting them both. The aedeagus has an armature and, unless the median plate be combined with this, it is absent. It is not certain if a ventral plate occurs.

MAIRA AENEA Fab.

Syst. Antl., 1805, 161 [*Laphria*]; Ricardo, *Ins. Samoa*, vi, 1929, p. 118.

This species is recorded as from North-east Australia by Ricardo in the above reference, and a series from the same locality is in the Deutsches Entomologisches Institut, Berlin-Dahlem.

Genus BATHYPOGON Loew.

Loew, *Prog. Realsch. Meseritz*, 1851, 13.

On the male, the dorsal lamella is divided and the ventral lamella is present. The aedeagus is short and attached for the full length to a broad armature and, being united, these are hinged to swing together; as the base is contiguous to the proctiger, there is no median plate. The ninth tergite is formed into upper forceps, and the lower forceps are short and very broad. The claspers are hinged. The ventral plate is rather broad and a pair of apical spine-like processes project from it.

On the female the dorsal lamella is divided and the ventral lamella is present but membraneous. The median plate is in two parts, anterior and posterior, both divided longitudinally; this form of median plate is one that is divided into four areas of chitin. The acanthophorites are present and between them the dorsal ridge lies detached. The genital groove is without chitin. A pair of plates containing supplementary spines is present, and these plates almost meet for a considerable distance along the median line, while two strong and two weak bristles lie at the outer area.

Judging from this form of the supplementary plates that bear spines, and that occur in various genera, many other genera have vestiges of them in the form of minute sclerites that have not been understood hitherto, and therefore were not specified in my account of the terminalia. In the more complete form they are present throughout the Therevidae and primitive genera like *Phellus* and *Erethropogon*, and are quite unknown to me outside the Asiloidea. Presumably they mark a primitive condition for the superfamily.

Genus STENOPOGON Loew.

Linn. Ent., ii, 1847, 453.

♀. The dorsal lamella is divided and the ventral lamella is present. The median plate is as on *Bathypogon*, as also are the plates that bear supplementary spines. These latter plates taper towards each other, ending in a point, instead of being broad along the

* Bromley cannot be correct in drawing his conclusion, for the evidence of structure indicates the origin of the tribe Laphriini may have been an ancient stock, the larvae specializing by following wood-boring beetles. The subfamilies Dasypogoninae and Laphriinae, as used by Bromley, do not mark natural divisions, the cleft originally thought to lie between these two major groups being non-existent, thus making unsatisfactory any criticism of general conclusions that may be drawn from the study of the complexes concerned.

median line. Acanthophorites and dorsal ridge are as on *Bathypogon*, and the genital groove has chitin at the base and a pair of small chitinous ridges near the apex.

RACHIOPOGON GRANTII Newman.

Trans. Ent. Soc. London, iv, 1857, 57.

On the male there are seven abdominal segments. The terminalia are bulbous and have a ventral plate. The species is the genotype and the genus is a complex as it now stands; owing to its rarity in collections, the present species is not adequately understood. The sexes are similar in general characters.

Hab.—Queensland: Brisbane. 1 ♂ taken by Mr. C. F. Ashby, near the Enoggera Reservoir, during November, 1938. As the unique type is lost, and without recorded sex, I have labelled this specimen the allotype male. Ricardo described the female, also from a unique, and this acts as a substitute for the holotype.

Genus CHRYSOPOGON Roder.

Berl. Ent. Zeit., xxv, 1881, 213.

On the male the dorsal lamella is divided and the ventral lamella is rather small. The median plate is absent and the aedeagus is simple. The ninth tergite is a simple sclerite. The lower forceps are developed and the claspers are fused to their support, The ventral plate is present.

The female terminalia show the dorsal lamella divided, and the ventral lamella rather small. The acanthophorites are large but without the spines, and the dorsal ridge is absent. The median plate is rather large and divided longitudinally. The genital groove is bordered with chitin on each side.

These characters are taken from a pair of small specimens of the *C. punctatus* Ric. form, captured at Goondiwindi (Q.), in October 1935, and the terminalia show the genus to have quite distinctive characters, especially in the acanthophorites which are intermediate between those bearing spines and those that tend to become obsolete.

CODULA LIMBIPENNIS Macq.

Dipt. Exot., suppl. 4, 1849, 70.—*Syn. C. vespiformis* Thomson, *Eugenies Resa Dipt.*, 1869, 464. For further references see Hardy, *Ann. Mag. Nat. Hist.*, (10) xvi, 1934, 32–33, where *C. vespiformis* was given as unrecognized.

Originally, in 1929 (*Proc. Roy. Soc. Qd.*, xli, 61), I had sunk Thomson's *vespiformis* to synonymy in the above manner, but there were several criticisms placed before me, including one emanating from the British Museum, which seemed rather conclusive, to the effect that Ricardo, at least, had been referring to two distinct species under these names.

In my 1934 paper, I had accepted this view, but since then have given further attention to this matter, and now conclude that my critics were led astray by recorded coloration. They have given too much importance to the moustache, said to be black in Macquart's description in contradistinction to yellow in Thomson's. We have the authority, however, of Ricardo's more recent description from Macquart's type, in which it is stated to be yellow, not black. Other discrepancies in descriptions are little more than may be expected by variations, not specific differences, and therefore I have returned to my original opinion that the two authors had but one species, for there is but the one species represented in every Australian collection that I have examined, and Macquart illustrated it.

LEPTOGASTER WHITEI, new name.

Leptogaster fumipennis White, *Proc. Roy. Soc. Tasmania*, 1913, 266, and 1916, 152; Hardy, *Ann. Mag. Nat. Hist.*, (10) xvi, 1935, 166.—nec Loew 1861 (Greece).

White evidently had a complex of species from his two descriptions under *L. fumipennis*, based on the female only. As the name is preoccupied, I take this opportunity to re-name the form described by me as being White's species. There can be no doubt that White's first description can apply only to this form. White states that he has seen the male, but it is not represented in his collection at the British Museum, and there is doubt whether White correctly allied it; it might belong to some other species

he had confused under the name, in his second description. The species is quite unknown to me outside Tasmania and it does not conform to the descriptions of any other Tasmanian species.

LEPTOGASTER ANTIPODA Bigot.

Ann. Ent. Soc. France, (5) viii, 1878, 445.—*Syn.*—*vernalis* White; *autumnalis* White; and *geniculatus* White, nec Macquart, Tasmanian specimen only.

It is not difficult to recognize Bigot's species from description, as "deux bandes médianes" can apply to only one of the three species in Tasmania, and to which White's *vernalis* and *autumnalis* apply as new and old season specimens respectively. The species is variable and White erroneously placed one under the name *geniculatus* Macq. which is recorded from Tasmania but probably was from Sydney and perhaps identical with *L. bancrofti* Ric. ♀. Ricardo's *geniculatus* is probably *L. pedanius* Walker, a species that extends from Sydney to Brisbane.

The present form is known to me only from Tasmania, as also is *L. aestiva* White, the third valid species.

ADDENDUM.

In a series of papers, "Notes on Australian Muscoidea", appearing in the *Proceedings of the Royal Society of Queensland*, it is my endeavour to bring that section of the Cyclorrhapha into a phylogenetical classification, as has already been done for the lower Brachycera, and these two groups are found to interlock in colour characters in a way that has led various authors to draw attention to remarkable resemblances between them, generally with views on the subject of "mimicry". This so-called parallel development in widely different families, seems to be due to the natural sequence of colour changes which takes place with the evolutionary trends of these flies and the colour changes are not developed in any way by any action of natural selection which authors are tending to show. The resemblances between certain Diptera and Hymenoptera may also be due to the natural sequence of colour changes, and natural selection could conceivably preserve such cases but could not have brought them into existence as many authors seem to think. I do not agree with Nicholson's claim (*Aust. Zool.*, v, 1927, p. 38)* that there was first a resemblance that deceived, and natural selection played upon this bringing it to perfection (a view that researches on genes do not uphold), and substitute the idea that the resemblances may have been preserved in cases where benefit is to be derived, wherever a mimic and model are coincident in colour developments.

It is pertinent to note that, wherever the Australian lower Brachycera are regarded as mimics, they are found to be rather low in the phylogenetical tabulation.

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* Nicholson conveys this idea throughout his paper, but I quote one passage: "Before natural selection can operate in the production of a mimetic form, it is necessary that the incipient mimic should first bear a sufficient resemblance to a suitable model to be mistaken for it occasionally, and the primary resemblance must necessarily be fortuitous."

In the present discussion, coloration is not regarded as a fortuitous factor, but is considered to develop in a natural sequence, the stage reached being identical in both mimic and model, whilst natural selection is in no way concerned in development of the mimetic type thus evolved, but might possibly play a part in maintaining its stability.

AN INVESTIGATION OF THE LIFE CYCLE OF *MACROZAMIA SPIRALIS* MIQ.

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(Plates xiv–xvii; ninety-three Text-figures.)

[Read 30th October, 1940.]

An investigation of the life-history of *Macrozamia spiralis* was begun early in 1938. Two main reasons governed the decision to embark on the work, first, the fact that up to that time little had been published regarding this particular genus, and second, notwithstanding the voluminous literature on cycads in general, many important phases in their life histories remain to be described. In 1939 the authors presented a preliminary account of megasporogenesis in *Macrozamia spiralis*, and since then Baird, A. M. (1939), has published the results of her researches on *Macrozamia Reidlei*. Other investigators, namely, Chamberlain (1913) on *Macrozamia Moorei* and Light (1924) on *Macrozamia Fraseri*, have made contributions to our knowledge of the genus, but it is believed that the present comprehensive account embodies many facts of particular interest, relative not only to *Macrozamia*, but to cycads in general. Only those features which are new, or of special significance, are stressed, although other facts necessary to preserve continuity, and to make comparison with other genera are included.

Distribution.

The genus *Macrozamia* is confined to Australia and, in those districts in which it is most abundant, is the dominant plant over very considerable areas. It then forms a much more prominent feature of the flora than either of the other endemic genera, namely, *Bowenia* and *Cycas*.

Macrozamia spiralis is widely distributed throughout the eastern coastal areas, extending from southern Queensland almost to the southern limit of New South Wales, a distance of approximately a thousand miles, and in number of individual plants probably exceeds that of any other cycadean species. Typically, it occurs in vast numbers in open eucalyptus forests from just above sea-level to a distance of several hundred yards inland. Occasionally, the species is encountered in isolated areas, each supporting some hundreds of plants, at a distance up to ten or fifteen miles from the coast, but, beyond that, this species is rare, although several small societies have been found as much as thirty miles inland.

Habit and Habitat.

Macrozamia spiralis finds its maximum expression on sand-dunes adjacent to the sea, or on ridges of light sandy soil formed by the disintegration of the underlying sandstone, or by wind-borne shore sand. In such an environment only the major portions of the leaves and the cones appear above ground. The lower parts of the petioles, the younger leaves, and the organic apex are buried in the soil, as are, of course, the thick tuberous stem and deep root system (Pl. xiv, figs. 2, 3).

More rarely a society flourishes on hard quartzite or sandstone ridges, but then the resistant nature of the subsoil—chiefly rock fragments—retards penetration, and the stem, encased in an armour of leaf-bases, rises above the ground exposing a trunk up to four feet high (Pl. xiv, fig. 4).

Such plants are almost as massive and well-developed as those on softer soils. A comparative study of plants at various stages of development indicates that the continued burying of the apex in the softer soils is due to the action of contractile roots (Text-figs. 89–93). In hard stony situations this contractile force is evidently unable to overcome the resistance of the sub-soil, and so the stems protrude well above ground level (Pl. xiv, figs. 4, 5).

A well-developed plant on the quartzite, then, may have a trunk protruding as much as four feet above the soil level, the extent of the region exposed being in direct proportion to the difficulty of penetration, while the lower part of the stem, and the root system, may extend for two or three feet underground. Accordingly, as is obvious in Plate xiv, figure 5, this form is more attenuated than that characteristic of the softer soils. The protection afforded the exposed stem by the stout persistent leaf-bases is of very decided value as a defence against the heat engendered by bush fires, which are liable to occur frequently on such a dry habitat. Even under the driest conditions the tissues are well supplied with water, and, if a cavity be cut in the sappy tissue just below the stem apex, moisture will gradually accumulate in the hollow.

The plants are dioecious. The number of cones produced during any one season by a staminate plant (Pl. xiv, fig. 3) is on the average in excess of that produced by an ovulate plant, the usual number for the former being three to four, while in the latter, two to three prevail (Pl. xiv, fig. 2). Extreme numbers for the above are seven to ten and five to six respectively. Generally, the dimensions of the cones on plants growing in soft soils are slightly greater than those produced by plants on the stony ridges.

Staminate and ovulate plants possess a similar appearance, and in the field can only be distinguished with certainty by the presence of cones, or by the occurrence of seeds, testas, or seedlings around the trunk of ovulate plants.

Strobili.

About the beginning of March the cones first become visible amid the crown of leaves. The majority of plants produce cones at the same time and these develop at about the same rate, but individual plants may lag a week or two behind their fellows.

Mature microsporangiate cones, that is, cones at the time of shedding pollen, have an average length of 38 cm. and a diameter of 10·2 cm. The corresponding dimensions of a seed cone are 35·6 × 19·0 cm., but a maximum measurement of 45 × 18 cm. with a weight of 5·77 kg. has been recorded by the writers. Some half dozen mature seed-cones, taken at random, had the following weights: 5·77 kg., 4·31 kg., 4·1 kg., 3·06 kg., 2·608 kg., and 2·154 kg., giving an approximate average weight of 3·6 kg. It is to be noted that in all these data the peduncle has been excluded. The youngest megasporangiate cone, collected on 27th December, 1938, weighed only 0·6 gram, while the microsporangiate cone of the same date weighed 0·7 gram. These records represent the result of field observations ranging from two hundred miles south to thirty miles north of Sydney.

The microsporangiate and megasporangiate cones originate about the same time. The seed cone takes about eighteen months to mature, while the microsporangiate cone sheds its pollen some five months earlier. It is estimated that cones are almost exactly twelve months old at the time of pollination, but a further five to six months elapse before the absciss layer, formed near the base of the megasporophyll, breaks down to permit the collapse of the cone and the dispersal of the seeds.

Macrozamia spiralis grows abundantly in the vicinity of Sydney. This fact makes it relatively easy to collect material at regular intervals over a period covering the phases of reproduction. As a general rule, fortnightly intervals were regarded as satisfactory, but during the more critical phases the intervals between successive collections were considerably reduced, until, in tracing megasporogenesis, fertilization and embryogeny, collections were made twice weekly.

The more mature cones were easily harvested, but the younger, such as those showing sporophyll primordia and megasporogenesis, are deeply sunken amid the apical leaves; consequently a more elaborate method of removal had to be adopted. This method is described fully in later pages.

Technique.

The material was fixed either in strong chromo-acetic solution or in Fleming's fluid, and having been transferred to paraffin wax was microtomed in the usual way.

Three different staining methods were used: (*a*) Haedenhain's iron-alum haematoxylin method, destaining with picric acid; (*b*) Newton's iodine method; and (*c*) Fleming's triple stain.

The first-named method was used throughout, the others only in cases where their adoption conferred some special advantage.

TABLE I.

The Megasporangiate Cone.

With the exception of the first two sets of readings, all data refer to cones from which the peduncle had been removed.

Date.	Dimensions (cm.). Length.	Breadth.	Weight (grams).	Sporangial Features.	General Observations.
27/12/38	1·5	0·8	0·6	Sporangium just visible to naked eye.	Cones hidden amid leaves near stem apex.
	with peduncle				
20/1/39	3·5	1·1	1·3		do.
	with peduncle				
31/1/39	3·8	1·5		Megaspore mother-cell stage to megaspore formation and young gametophyte.	do. Integument up to shoulder of nucellus.
11/3/39	12·0	3·7		Early free nuclear stage of gametophyte.	Apices of cones just visible amid vegetative leaves; nucellus enclosed by integument.
14/4/39	16·3	4·8		Advanced free nuclear stage of gametophyte.	Cones protruding about three inches.
13/6/39	17·2			Wall formation in gametophyte almost completed.	Prominent nucellar beak protruding far into micropyle.
10/7/39	19·6	7·5		Wall formation in gametophyte completed.	Gametophyte cells under high pressure and at jelly stage.
16/8/39	19·8	7·6			Archegonial initials present.
3/9/39	23·0	10·2		Solid gametophyte tissue.	Archegonia with neck cells beginning to enlarge.
2/10/39	25·4	11·3			Some ovules near base and apex of cone have aborted.
29/10/39	25·6	14·2		Gametophyte measures 1·7 cm. × 1·2 cm.	Archegonia arranged in a ring in distinct archegonial chambers. Ovules assume pale pink colour.
12/11/39	28·0	14·9		Archegonia enlarged and highly vacuolate.	Sporophylls separated; pollination completed; microspores in shallow pollen chamber.
10/12/39	28·5	14·9		Neck cells protruding into archegonial chamber.	Integuments becoming stony. Sporophylls more widely separated.
31/12/39	38·1	20·3	3629	Archegonia in deep chamber; male gametophyte almost mature.	Ovules bright scarlet.
14/1/39	41·7	19·0	5670	Grand period of fertilization.	Specially long cone; average wgt. of 6 cones was 3742 gm.
29/1/39	30·4	17·4		First division of zygote.	Cones vary greatly in size; ovule-bearing region of sporophyll now very massive.

TABLE I.—*Continued.*

The Megasporangiate Cone.—Continued.

Date.	Dimensions (cm.). Length.	Breadth.	Weight (grams).	Sporangial Features.	General Observations.
4/2/40				Proembryos showing incipient wall formation.	Cone axis elongates with separation of sporophylls; abscission layer apparent.
5/3/40				Embryos at various stages up to appearance of the two cotyledons.	Sporophylls detached from cone axis owing to collapse of abscission layers.
1/6/40				Average number of viable seeds per cone is 126. Average number of aborted ovules per cone is 15·1 per cent.	Number of sterile megasporophylls at apex and base respectively of cone averages about 20.

TABLE II.

The Microspongiate Cone.

All data, except first reading, have been made from cones with peduncle removed.

Date.	Dimensions (cm.). Length.	Breadth.	Weight (grams).	Sporangial Features.	General Observations.
28/12/38	1·9	0·8	0·7 with peduncle		
3/2/39	6·0	2·1	11·0		
11/3/39	9·0	2·6		Walls and sporogenous cells differentiated. Tapetum not evident.	Cones hidden amid apical leaves, sori of 3 to 4 sporangia, crowded on lower surface.
14/4/39	12·0	3·5		Sporogenous cells and tapetum present.	Cone tips visible amid apical leaves.
13/6/39				Dehiscence mechanism differentiated; spore mother-cells in prophase.	Cones conspicuous amid apical leaves; sporophylls closely packed; distinct line of dehiscence.
10/7/39	18·5	8·4		do.	
6/8/39	20·5	8·6		Heterotypic division at metaphase, to tetrad formation.	Slight separation of sporophylls by elongation of cone axis.
17/9/39	30·0	13·5		Young microspores.	Sporophyll separation more pronounced.
12/11/39	38·5	12·5		Gametophyte mostly at three-nucleate stage.	Sporophylls widely separated; dehiscence of sporangia in progress or completed.
10/12/39	32·9	7·0		Male gametophyte developing in pollen chamber.	Empty sporangia; cone drying out and contracted.
1/6/40				Average number of sporangia per sporophyll is 342.	Average number of sporophylls per cone is 345. Number of sterile sporophylls at base and apex of cone respectively averages about 20.

The Megasporangiate Cone.

The youngest cones were procured on 27th December, 1938. Their average dimensions including peduncle were length 1·5 cm. and breadth 0·8 cm., while the weight was 0·6 gram. The ovulate plant typically produces two such strobili, but three or four are not uncommon. Any number beyond this is rare. The cones arise laterally around the growing point in the manner indicated in Plate xvi, figure 11, and are approximately of the same age and dimensions.

The apex of the plant is persistent, and near the organic apex bears numerous whitish-yellow leaves of very soft texture which, like the sporophylls, arise in acropetal succession and are spirally arranged. These young leaves are so delicate that they are unable to support their own weight, being held in position by the enfolding leaves, which, with age, assume a stiffer texture. The cones are approximately at the same level, and each is ensheathed in, and protected by, a large number of spirally arranged, specialized, vegetative leaves, fawn to brown in colour and bearing on the outside a dense soft woolly covering of hairs. The whole forms a bud-like structure about twelve inches in height. The outer protective leaves terminate in long spine-like tips (Text-figs. 3, 4, 5; also Pl. xvi, figs. 11, 12). Each strobilus, then, is most efficiently guarded against desiccation and sudden changes in temperature. Text-figure 2 gives some idea of the shape and size of one of these minute cones, while Text-figure 1 depicts a strobilus, amid its protective leaves, the upper parts of which have been excised, in order to expose the tip of the cone. Even in the youngest cones inspection with a lens of the basal region of the sporophyll reveals two minute protuberances, each the primordium of a megasporangium.

Thereafter, during each successive month, cones were collected and data relative to their gross development recorded. For ease in reference, and to facilitate comparison, the results obtained have been tabulated and presented in condensed form in Table i, where the various developmental stages are set out. Comparison with Table ii permits a ready appreciation of the relative rates and stages of growth of the megasporangiate and microsporangiate cones.

The difficulty in obtaining the more minute cones is well known to all familiar with cycads, and is attested by the paucity of information regarding them. Accordingly, it may not be unprofitable to indicate how, in the case of *Macrozamia spiralis* at least, one may detect their presence with certainty, and so prevent unnecessary destruction of plants, not to mention vexatious waste of time and labour.

In the first place, plants which bear exposed cones are avoided, as experience has shown that in no case have these begun the production of new cones—an interval of a year or more elapses. Seedlings, mature seeds or empty testas indicate the carpellate plant. Next, the mature leaves of an approved specimen are forced downward and outward as far as possible, in order to expose the younger central leaves. These in turn are carefully separated, and the investigator looks for the hard brown tips of the protective leaves encircling each cone. Only the sharp brown withered-looking tips will be apparent. One or more groups of such spines may be observed, and these in a position lateral to the region producing the young, apical, yellowish, vegetative leaves. On account of their close packing, it is not difficult to distinguish such groups from the now widely-spread persistent, protective leaves, associated with defunct cones of some previous season. Thereafter, a trench some two feet deep is dug about half-way around the plant so as to expose the tuberous region and persistent leaf-bases. Then, using a sharp axe, slices roughly tangential and vertical are chopped gradually away, until the central region is approached. In this way the characteristic protective leaves of the young cones are exposed, and by pushing these aside the strobili may be excised without injuring the central growing region (Pl. xiv, fig. 6). The soil may then be replaced, and the plant given an opportunity to recover.

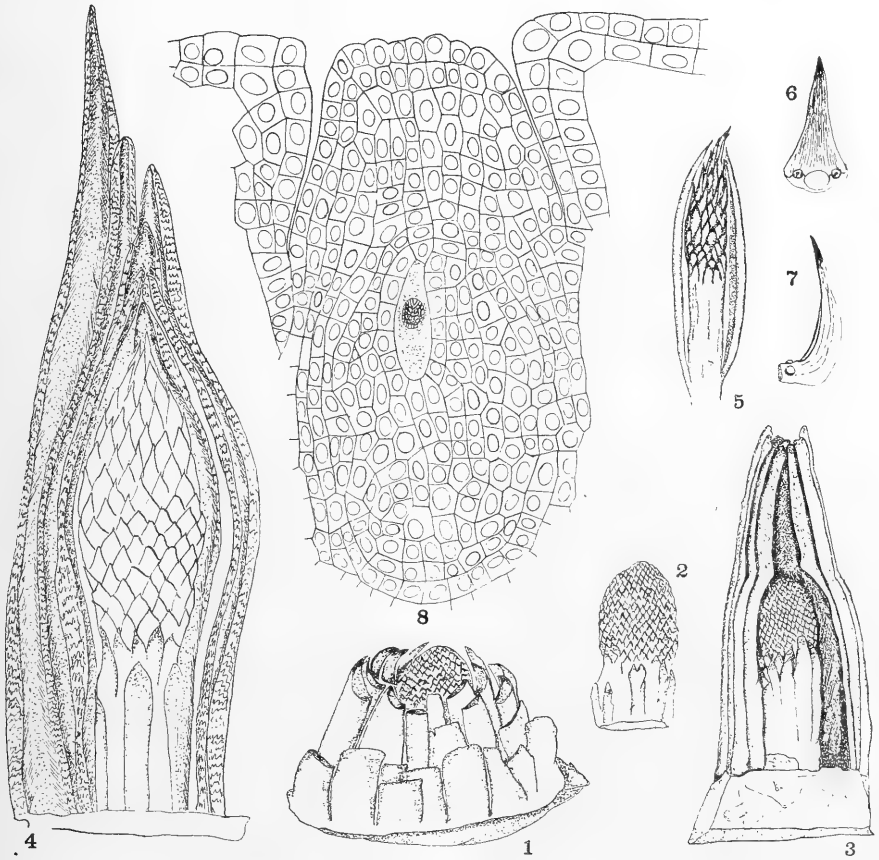
Megasporogenesis.

The megasporophylls, as in all cycads, are arranged spirally and in acropetal succession (Text-fig. 4). By careful dissection of the very young cones referred to above,

the individual sporophylls, each bearing two minute megasporangia marginal in origin and adjacent to the cone axis, were separated (Text-figs. 6, 7).

A median vertical section of such a sporangium revealed the presence of a megaspore mother-cell, deeply sunken in the tissue of a massive nucellus which, in turn, was partly enclosed by the young integument (Text-fig. 8).

The mother-cell was most conspicuous on account of its size, prominent nucleus, and typically elongated shape. In its cytoplasm was embedded a large number of starch grains, specially abundant towards the chalazal end (Text-fig. 9). Examination of the megaspore mother-cell, contained in each of a considerable number of sporangia, from the same and from different cones, revealed the nucleus as almost always in the



Text-fig. 1.—Top of minute ovulate cone apparent amid the overlapping protective leaves, the upper portions of which have been excised. 28 Dec., 1939. × 1·6.

Text-fig. 2.—Another cone from same plant as in previous figure showing fertile zone and peduncle bearing several scale leaves. 28 Dec., 1939. × 1·6.

Text-fig. 3.—A microsporangiate cone showing scale leaves growing from basal region of peduncle, the whole enclosed in a chamber formed by the overlapping and closely packed protective leaves. 28 Dec., 1939. × 1·6.

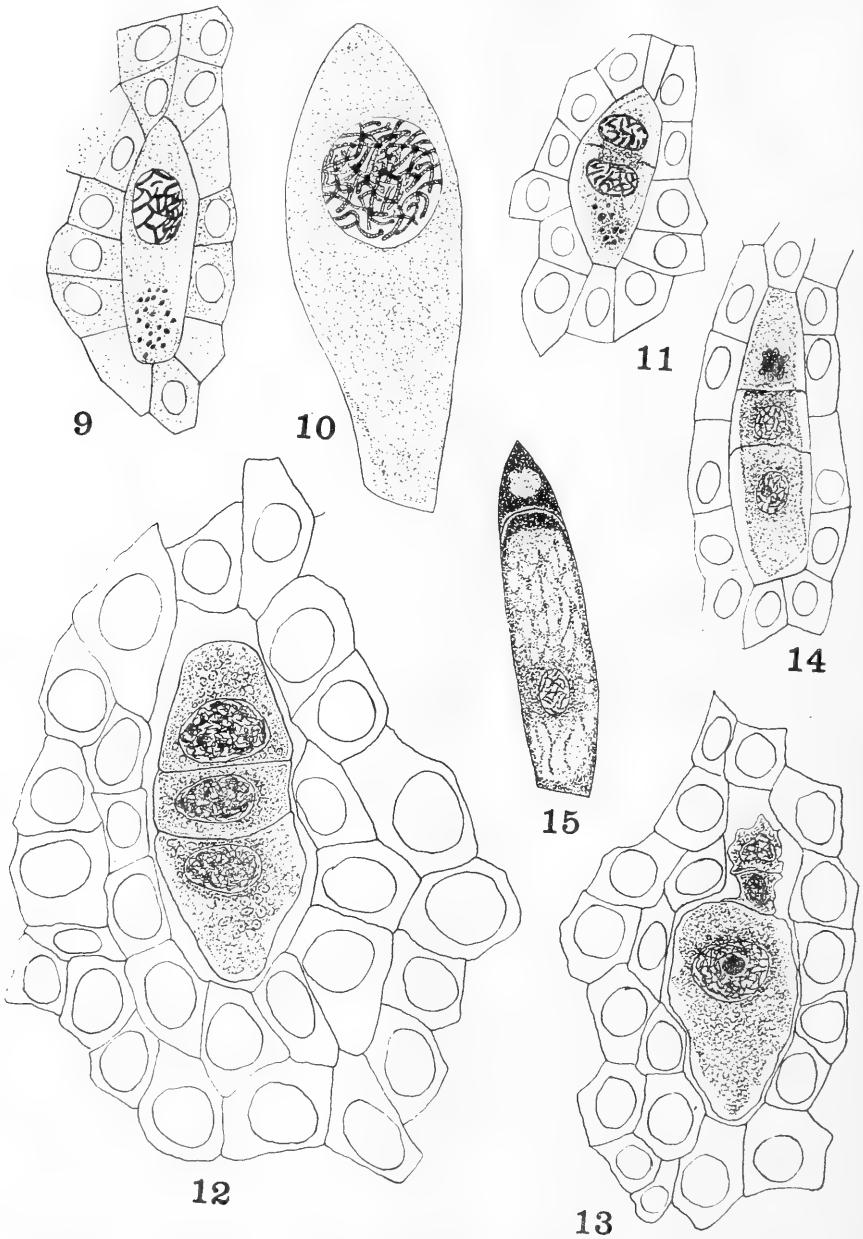
Text-fig. 4.—Lateral megasporangiate cone, bearing scale leaves and enclosed by protective leaves. 20 Jan., 1940. × 1·6.

Text-fig. 5.—Ovulate cone five weeks older than that depicted in Text-figure 2. All the protective leaves except two have been removed. 31 Jan., 1940. × 0·4.

Text-fig. 6.—Adaxial view of megasporophyll showing marginal position of the two young ovules. 20 Jan., 1940. × 4.

Text-fig. 7.—As above but in profile. 20 Jan., 1940. × 4.

Text-fig. 8.—Median longitudinal section of very young megasporangium partly enclosed in young integument. The relatively large deeply-sunken cell with conspicuous nucleus is interpreted as the megaspore mother-cell. 31 Jan., 1939. × 34.



Text-fig. 9.—Longitudinal section of megaspore mother-cell embedded in nucellar tissue. Starch grains are apparent at end adjacent to chalaza. 31 Jan., 1939. × 490.

Text-fig. 10.—Another megaspore mother-cell. The chromatin is segmenting and the nucleus is evidently about to undergo division. 31 Jan., 1939. × 800.

Text-fig. 11.—Binucleate condition resulting from division of nucleus at stage represented in Text-figure 9 or 10. A thin wall separates the nuclei, and starch grains are present in lower cell. 31 Jan., 1939. × 490.

Text-fig. 12.—A three-nucleate condition attained by division of the nucleus adjoining the chalaza in previous text-figure. 31 Jan., 1939. × 710.

Text-fig. 13.—View of the persistent functional megaspore which has increased in size. The sister megaspore, and the third or micropylar nucleus are disintegrating, but the original dividing walls are still evident. 31 Jan., 1939. × 710.

Text-fig. 14.—Another view of the three-celled stage in which the nucleus adjacent to the micropyle is beginning to disintegrate. × 710.

Text-fig. 15.—The functional megaspore capped by the remains of the two evanescent cells. 31 Jan., 1939. × 490.

resting condition. However, in a few cases (see Text-fig. 10), the chromatin had thickened and commenced segmentation, while in one particular case, individual chromosomes were recognized, although their exact number was not determinable. Unfortunately, despite persistent search, the material sectioned did not reveal the spindle formation which should normally ensue. None the less, the subsequent binucleate stage was identified (Text-fig. 11), the nuclei being separated by a thin wall. No wall, however, was recorded, for the corresponding stage, by Smith (1910) in the case of *Zamia floridana*. Thereafter, the chalazal nucleus divided, and a row of three cells resulted (Text-fig. 12), as compared with the four for *Zamia* (Smith, 1910) and three for *Stangeria paradoxa* (Lang, 1900). Numerous preparations were made and examined, but in no case was the micropylar nucleus found to divide. Accordingly, the writers are of opinion that the three walled-cells in a row represent the full progeny of the spore mother-cell.

Subsequently, the chalazal cell enlarged, and the nuclei of the other two cells gradually disintegrated, the evanescent cells forming a densely-staining cytoplasmic cap at the micropylar end of the functional and enlarging megaspore (Text-figs. 13, 14, 15). Clearly, the surviving nucleus was that of the functional megaspore.

At this stage, it is appropriate to call attention to the fact that Professor J. C. Chamberlain, referring in the course of correspondence to the writers' earlier account of megasporogenesis (Brough and Taylor, 1939), made the following pertinent observation: "You speak of a row of three megaspores; when you stop to think about it, only two of the three are megaspores; the third, unless it divides, is still a 2x structure and has not yet reached the megaspore stage."

Accordingly, in the present account, the writers have refrained from referring to the three cells in question as megaspores, although this procedure does not necessarily imply abandonment of the view previously expressed.

Only a demonstration of the actual chromosome sets involved will determine with certainty the correct constitution of the nuclei concerned. This, in turn, will furnish an answer to the critical question as to when reduction division actually takes place, and so finally decide which cell is the spore mother-cell and which cells are megaspores.

Female Gametophyte.

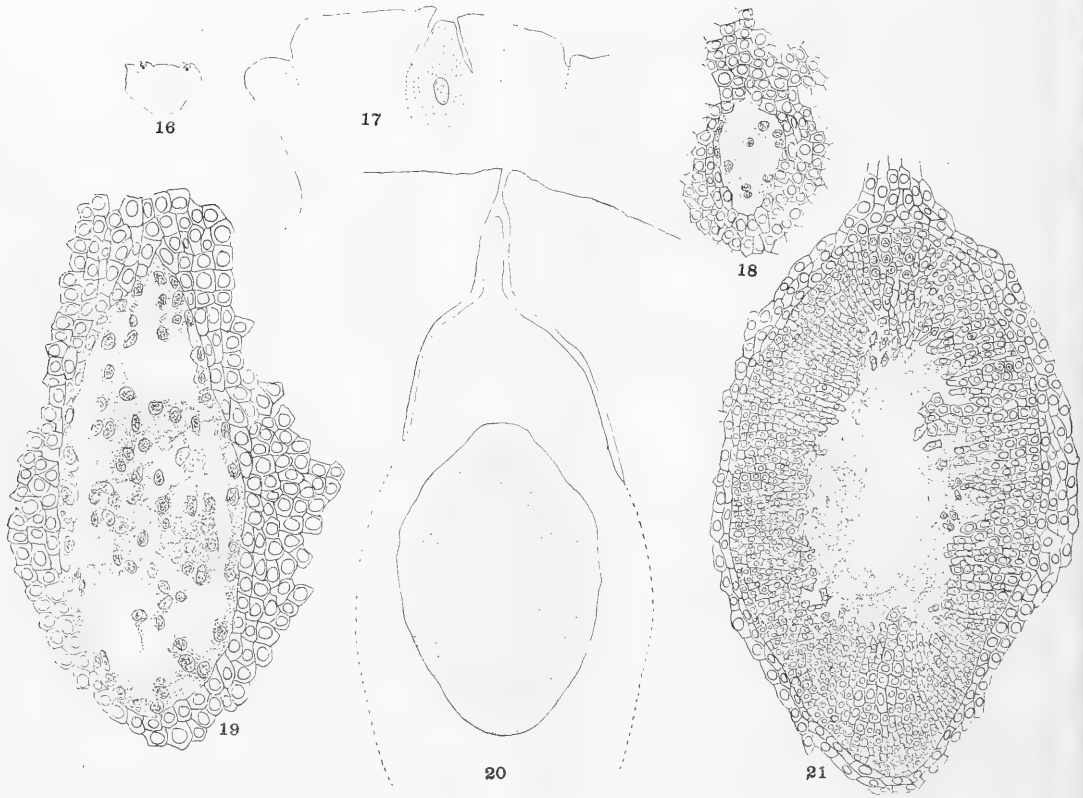
The functional megaspore without any resting period develops into the young gametophyte (Table i). Text-figure 16 shows a megasporophyll in surface section bearing two ovules, each of which contains such a gametophyte with several nuclei embedded in the cytoplasm within the megaspore membrane. A later stage under higher magnification is depicted in Text-figures 17 and 18. In these cases the cytoplasm is slightly vacuolate, and the number of nuclei has increased. Text-figure 19 illustrates portion of an even more advanced stage. The gametophyte has increased greatly in size, while the numerous nuclei are embedded in increasingly vacuolated cytoplasm. The section is not median, hence the prothallus is shown partly in tangential view. It is evident, however, that wall formation has commenced in contact with some regions of the megaspore membrane. Further development proceeds rapidly (vide Table i) until the gametophyte is represented by a layer of tissue lining the megaspore membrane, and enclosing a large central vacuole. Thereafter, wall-formation is continued and centripetal growth proceeds apace (Text-figs. 20 and 21) until finally a continuous mass of cells, rich in starch, fills the entire space within the membrane.

At this stage the jelly-like tissue is under exceedingly high pressure and, when punctured, the contents spurt out with considerable force.

The Archegonium.

The course of development of the archegonium was found to correspond in the main with accounts already published of this structure in other cycads. The archegonial initials were discernible about the time that wall-formation in the gametophyte was completed. In the apical region of the prothallus an initial is recognized by its larger dimensions relative to the surrounding cells, and prominent nucleus (Text-fig. 22). This initial enlarges, the nucleus dividing to give an outer or primary neck-cell and an inner cell (Text-fig. 23). The former then divides by an anticlinal wall, thus

initiating the two young neck-cells (Text-figs. 24 and 25). The inner cell, meanwhile, increases enormously in size, the cytoplasm becoming denser but containing very numerous vacuoles of varying dimensions, which impart the frothy appearance depicted in Text-figure 26. During this period the contiguous cells, distinguished by the regularity of their arrangement and the density of their contents, become conspicuous and constitute the archegonial jacket (Text-figs. 23–26). While these changes are being effected, a depression, known as the archegonial chamber, is forming at the micropylar end of the gametophyte. Archegonia are visible on the floor of this chamber (Text-fig. 27), where the neck-cells of five archegonia are clearly in evidence. In this connection, it may be mentioned that the writers encountered several cases of malformed or irregular chambers. Text-figures 28 and 29 illustrate two typical cases.



Text-fig. 16.—Section cut parallel to adaxial surface of sporophyll to show the marginal position and general structure of the two young ovules. The integument, nucellus and position of the young gametophyte are indicated. 31 Jan., 1939. × 2⅔.

Text-fig. 17.—One of the ovules in previous figure under a higher magnification. 31 Jan., 1939. × 40.

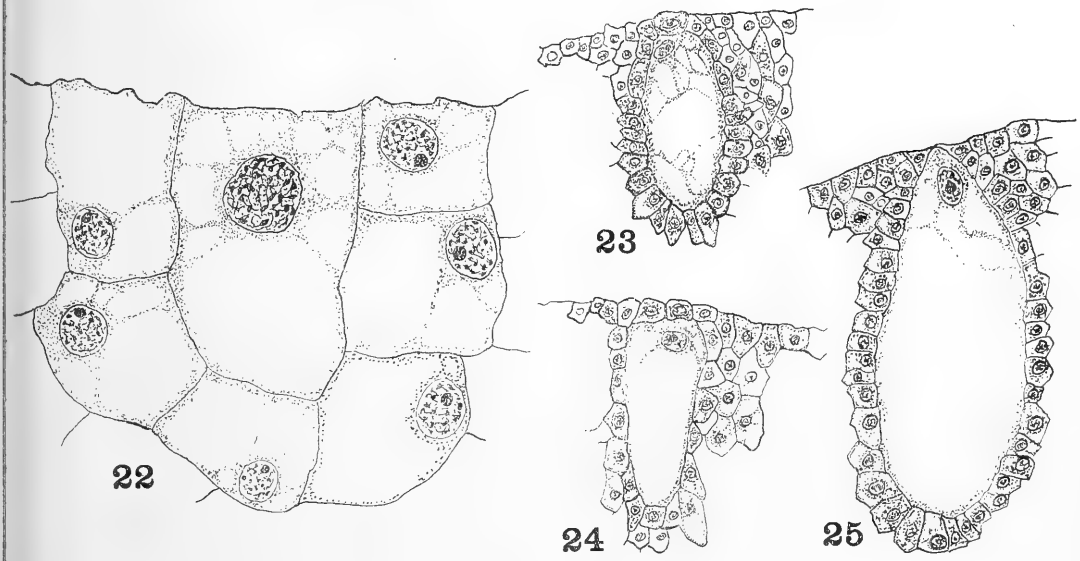
Text-fig. 18.—High-power study of part of ovule depicted in Text-fig. 16, showing young female gametophyte at early free-nucleate stage. The nuclei are embedded in a peripheral layer of cytoplasm enclosing a central vacuole. 31 Jan., 1939. × 180.

Text-fig. 19.—A somewhat later stage of development of the prothallus cut longitudinally. The gametophyte has increased greatly in size while the numerous nuclei are embedded in the vacuolated cytoplasm. Wall-formation has commenced against some regions of the megaspore membrane. Section is more or less tangential. 11 Feb., 1939. × 180.

Text-fig. 20.—Median longitudinal section of ovule showing integument, nucellus with long beak protruding into micropyle, and female gametophyte. Note great increase in size since 31 Jan., 1939. × 40.

Text-fig. 21.—Median longitudinal section through female gametophyte of previous text-figure. The regular centripetal growth of the original peripheral cells is strongly emphasized, and the invasion of the central vacuolate region is about two parts completed. The tissue within the original megaspore membrane has increased enormously in size and is of a jelly-like consistency. × 180.

In the first, the chamber bearing eight archegonia is crescent-shaped with a raised part in the centre, while in the other the archegonia are in two separate compartments, one partial chamber with four and the other with three. Such chambers are not regarded as having any special significance.



Text-fig. 22.—Median longitudinal section of archegonial initial, which is vacuolate, has a large nucleus, and is of greater dimensions than the contiguous cells which later form a conspicuous jacket. 16 Aug., 1939. × 710.

Text-fig. 23.—Median longitudinal section of a young archegonium showing primary neck-cell just before division and also the central cell; the nucleus of the latter adjoins the primary neck cell. The cytoplasm of the central cell shows numerous vacuoles. An archegonial jacket is evident. 16 Aug., 1939. × 100.

Text-fig. 24.—Median longitudinal section of a slightly older archegonium. In this case, the primary neck-cell has divided, giving rise to the two neck-cells of the mature archegonium. 16 Aug., 1939. × 100.

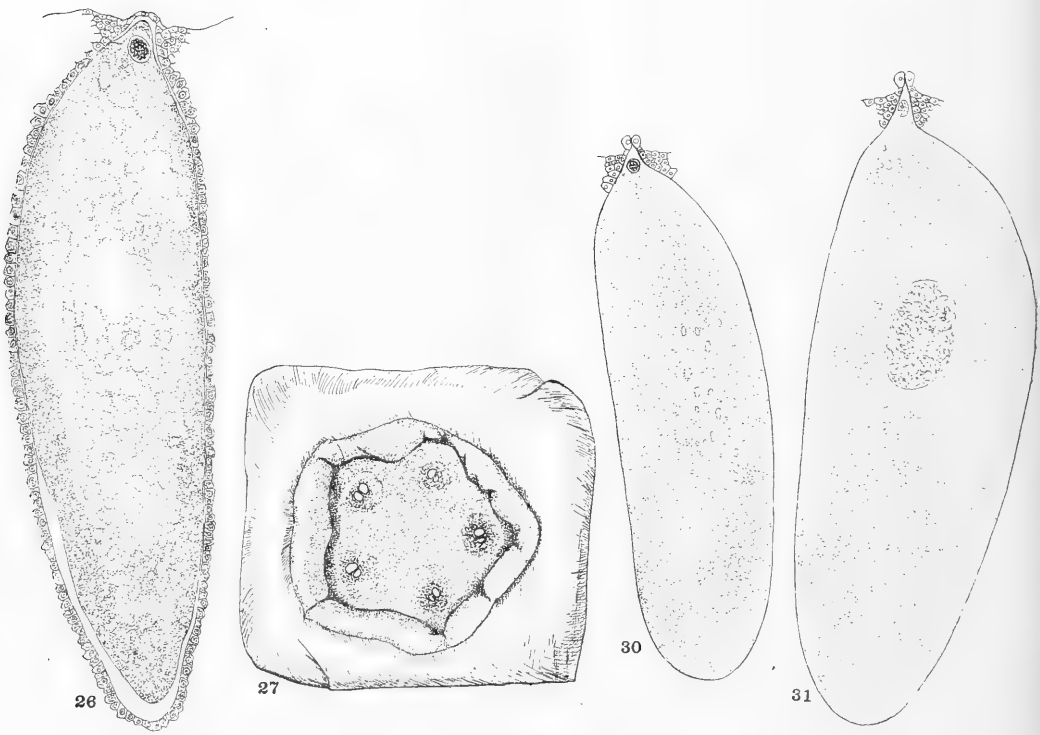
Text-fig. 25.—An archegonium, slightly older than that depicted in previous figure. The section is not quite median and the neck-cells are not in evidence. The archegonial jacket is now clearly differentiated. 17 Sept., 1939. × 100.

At the stage when the inner cell of the archegonium shows maximum vacuolation, the nucleus is characteristically located close to the two neck-cells which, up to this time, are relatively insignificant in size. However, the immediately subsequent development is marked by enormous increase in dimensions of the neck-cells which now protrude bodily into the chamber. Meanwhile the vacuoles of the inner cell have been steadily decreasing in number and size (Text-fig. 30).

The nucleus of the large inner cell does not long retain its identity for, on the same cone, cases are found where this condition, owing to mitotic division of the single nucleus, has been succeeded by the two-nucleate phase. These two nuclei are named the ventral canal-nucleus and the egg nucleus respectively. The former remains small and occupies the position originally held by the parent nucleus, while the latter has not only increased enormously in size, but has taken up a position about the centre of the cell. In addition the cytoplasm has become much more evenly granular, while the fast-disappearing vacuoles are relatively few in number (Text-fig. 31).

The dilated neck-cells, in longitudinal and transverse section, are shown in Text-figures 32 and 33 respectively. Each is vacuolate and provided with a prominent centrally placed nucleus. The relative thinness of the uniform wall is emphasized by comparison with the conspicuous egg-membrane, which has been undergoing a steady process of thickening during development. This thickening is interrupted by numerous

wide pits, through which coarse connecting strands of cytoplasm extend. Typically, the primary neck-cell divides once, but the process need not stop there, as is revealed by the fact that this investigation brought to light certain cases in which the subsequent division of the two neck-cells resulted in the formation of a neck consisting of four cells. Text-figure 34*a* shows such a neck in transverse section, while Text-figure 34*b* illustrates the same structure but with the cells separated in such a manner as to enclose a central canal. Necks comprising more than two cells have already been recorded for *Encephalartos villosus* by Sedgwick (1924), who figures as many as six. In one case the writers found a single chamber containing four archegonia, each with a neck composed of four cells. This may be of some significance in view of the general similarity between *Macrozamia* and *Encephalartos*, a similarity which may find its origin in a close relationship. A computation of the number of archegonia occurring within different chambers in numerous ovules selected from various cones gave the following results:



Text-fig. 26.—Later stage in development of the archegonium. Two neck cells are evident and their nuclei are relatively small in comparison with the large nucleus of the central cell which lies near the neck. The very numerous vacuoles give the cytoplasm a frothy appearance. A very pronounced layer of nourishing cells, forming the jacket, invests the central cell. 29 Oct., 1939. × 50.

Text-fig. 27.—Surface view of the archegonial chamber at apex of female gametophyte. The rim of the chamber slightly overhangs the cavity, on the floor of which five protruding twin neck-cells are apparent. 8 June, 1939. × 8½.

Text-fig. 30.—An advanced stage of archegonial development in which the archegonium has almost attained mature size. The vacuoles are considerably reduced in number and size. The neck-cells are dilated and project prominently above the floor of the archegonial chamber, while the nucleus lies in the attenuated apex of the central cell. 21 Nov., 1939. × 28.

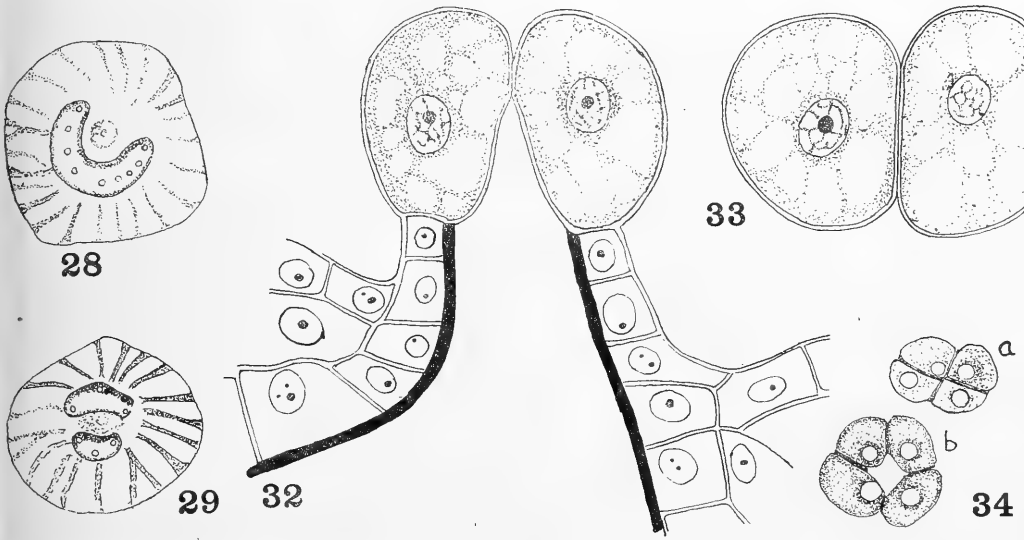
Text-fig. 31.—Median longitudinal section of an archegonium which differs from that of the previous figure in that the central cell nucleus has already undergone division giving the ventral canal nucleus and the enormous egg-nucleus. 21 Nov., 1939. × 28.

Percentage of ovules with	3	archegonia	=	13·0
„	„	„	„	4	„	=	39·5
„	„	„	„	5	„	=	40·0
„	„	„	„	6	„	=	6·0
„	„	„	„	7	„	=	1·0
„	„	„	„	8	„	=	0·5
							100·0

The Microsporangiate Cone.

The microsporophylls arise in acropetal succession and are arranged spirally on the axis (Pl. xv, fig. 8*b*). They vary considerably in shape and size according to their position on the cone, the most noticeable difference being the greater length of the spine-like terminal portions of the upper sporophylls (Pl. xv, figs. 10*a*, 10*b*). Again, despite the fact that the microsporangiate cone is much less bulky than the megasporangiate (Tables i and ii; and Pl. xv, figs. 8*a*, 8*b*), it none the less bears a much greater number of sporophylls. Actual counts from representative cones of each kind showed the microsporangiate cone to bear from 300 to 450 sporophylls, while the ovulate cone produced only from 70 to 105.

The youngest cones observed were collected on 28th December, 1938. These minute strobili with peduncles attached (Text-fig. 3) had the following average dimensions: length 1·9 cm., breadth 0·8 cm., while the average weight was 0·7 gm. In size and general appearance they somewhat resemble the microsporangiate cones of *Pinus*, and have, near the base of the peduncle, similar scale leaves to protect the very young sporophylls. Typically, the cones occur in groups of three or four, and always in a



Text-fig. 28.—An abnormal crescent-shaped archegonial chamber in surface view. Nine archegonia are indicated. 8 June, 1939. × 1¾.

Text-fig. 29.—Another abnormal archegonial chamber which consists of two subsidiary compartments, each bearing archegonia. 8 June, 1939. × 1¾.

Text-fig. 32.—Median vertical section through two greatly distended neck-cells, whose uniformly thin walls, highly vacuolate nature, and large size are evident. When these cells are fully extended they only impinge over a relatively small part of the opposing areas. 21 Nov., 1938. × 320.

Text-fig. 33.—Transverse section through the two neck-cells. 21 Nov., 1938. × 320.

Text-fig. 34.—Transverse section of an abnormal neck consisting of four cells investing a short canal, through which, in this case, the sperms probably gain entrance to the egg. (*a*) shows neck-cells in closed position; (*b*) shows neck-cells, 10 minutes after opening, with central canal. 10 Jan., 1939. × 70.

position lateral to the growing point. Their rate of growth is relatively fast, as exemplified by the entry in Table ii of data relating to a cone collected in early February, by which date the dimensions were, length 6·0 cm., breadth 2·1 cm., while the weight was 11·0 gm.

The above, and all succeeding data, concerning the strobili exclude the peduncle. Again, cones collected in mid-March average 9·0 cm. in length and 2·6 cm. in diameter (Pl. xvi, fig. 13).

At this stage the soral arrangement is evident, there being typically three to four sporangia per sorus, the former number, however, predominating. Inside each sporangium an undifferentiated mass of sporogenous cells is found, but without any evident tapetum.

An appreciation of the subsequent stages in development, terminating in the mature cone, may be gained by a study of the relevant columns in Table ii.

The Microsporophyll.

A series of photographs illustrating the size of the microsporophyll at different times of the year as compared with the size of the megasporophyll at the same dates is presented in Plate xvi, fig. 15, *a–d*, and Plate xv, fig. 9, *e–h*.

The relatively smaller size of the oldest microsporophyll is due to shrinkage consequent upon drying out after dehiscence of the sporangia and pollen dispersal. Again, the microsporophylls may remain attached to the cone axis for a year or more after pollen distribution, but the megasporophylls normally fall from the axis some five months after pollination, a discrepancy due to the early disintegration of the cells of the prominent abscission layer of the megasporophyll.

The Microsporangium.

On younger sporophylls, as already indicated, the sporangia occur in soral groups of three or four. On further development, however, such definite arrangement becomes progressively less distinct and finally unrecognizable. This may be explained by displacement and changed orientation of the individual sporangia consequent upon their greater increase in size not being fully balanced by synchronous growth of the sporophyll.

The number of sporangia per sporophyll varies with the position of the sporophyll on the cone. Some idea of the range of this inconstancy was obtained from actual counts which gave the following results:

Average number of sporangia on sporophyll near tip of cone	275
„ „ „ „ „ „ „ middle „	385
„ „ „ „ „ „ „ base „	255

In addition it was observed that the highest number of sporangia encountered on any one sporophyll was 412, while the lowest count was 195.

The shape of the sporangium in surface view varies from round to elliptical, the latter form becoming more pronounced as the pressure due to enlargement of contiguous sporangia increases (Pl. xv, figs. 10*a* and 10*b*).

The line of dehiscence first becomes discernible in early June, and is defined by the differentiation of a band of tissue, four cells broad, which becomes distinct owing to the relatively small size and thinner walls of its component cells (Text-fig. 37).

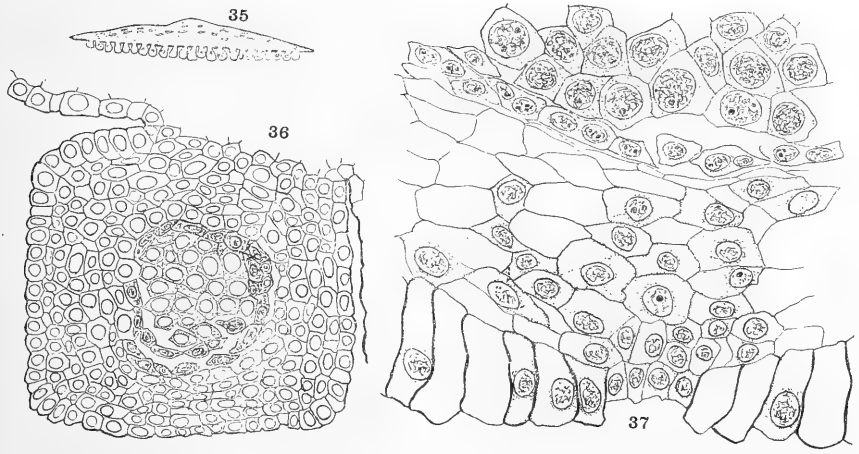
At maturity, usually during late October and throughout November, these cells break down, thus enabling the sporangium to gape widely and so liberate the pollen grains which are shed as a fine, powdery, cream-coloured mass (Pl. xv, fig. 10*b*). This dispersal is continuous over a period of several weeks because the sporangia open progressively throughout October and November, when the pollen gradually sifts out between the sporophylls.

The lightness of the abundant microspores renders them easy of distribution by wind action, which transfers them to the open micropyles of ovules now ready for reception.

In view of the fact that numerous accounts of the development of the cycadean microsporangium—from the stage of the sporogenous tissue to the production of mature

spores—have already been made, for example by Baird (1939), Chamberlain (1909), Lang (1897), and Smith (1907), it will suffice in the present instance to present only the more significant features.

Text-figure 35 is a transverse section of a microsporophyll collected in March. It is cut at right angles to the long axis, and portrays the shape and arrangement of the sporangia in vertical section, as well as their size relative to the thickness of the sporophyll. Numerous mucilage sacs are also in evidence.



Text-fig. 35.—Transverse section of young microsporophyll: hand-cut section showing arrangement of microsporangia on abaxial surface of thick, woody sporophyll. 13 June, 1939. × 2.

Text-fig. 36.—Longitudinal section of a young microsporangium showing massive wall of regularly arranged cells in which the line of dehiscence has not yet been differentiated; the central zone of sporogenous tissue is distinct, its cells having large nuclei and dense contents; a zone of tapetal cells already surrounds the central tissue: these cells are tangentially elongated and somewhat irregularly arranged. 14 April, 1939. × 180.

Text-fig. 37.—High power study of portion of longitudinal section of an older sporangium. The epidermal cells have differentiated, the majority being large, elongated, and radially thickened. A row of four cells in the central region of the wall, however, has remained small and thin-walled and defines the region of dehiscence. The inner cells of the wall are crushed, the tapetal zone is conspicuous, and encloses the large polygonal thin-walled densely cytoplasmic microspore mother-cells. 13 June, 1939. × 360.

The succeeding Text-figure shows a high-power study of a single one of these sporangia cut in a plane at right angles to the sporophyll. The wall, including the tapetum, is seven cells thick. The tapetal cells are elongated tangentially, and usually multinucleate. Although the layer is quite clearly differentiated, it at no stage assumes the prominence of that characteristic of similar structures in angiosperms. The specialized cells, which later determine the line of dehiscence, have not yet been differentiated. Some three months later the spore mother-cells are formed. These at first are close packed (Text-fig. 37) but later float separately in a nutritive matrix.

Their subsequent cytological history up to the formation of the mature microspores was traced, but the sequence of events conformed so closely with those already recorded for the corresponding phases in other cycads that it has not been deemed advisable to recall our observations here.

About the period of meiosis the tapetum commences to break down, as do certain of the inner cells of the wall, but even at maturity the wall is some four to five cells thick.

The abaxial epidermal cells, excluding those which constitute the region of dehiscence, are of a brownish colour with the radial and inner tangential walls considerably thickened, while the epidermal cells of the adaxial surface, that is, the region towards the stalk of the sporangium, are yellowish and thinner walled.

Dehiscence is due to the drying and contraction of these latter cells which exert a downward pull on the indurated cells towards the apex, and this in turn leads to the tearing apart of the band of cells which defines the actual line of dehiscence.

This account agrees with that given for *Stangeria paradoxa* (Lang, 1900) except for the fact that in the case of *Macrozamia spiralis* the band of cells governing the line of dehiscence is four cells broad instead of two as in *Stangeria parádoxa.*

The Early Male Gametophyte.

As a result of meiosis uninucleate microspores (Text-fig. 39) are normally produced in the microsporangium during late August. On division, which typically occurs during October, this nucleus produces a centrally placed tube nucleus and a second one close to the wall of the spore (Text-figs. 40 and 41). This latter nucleus, usually in November, divides in turn, giving a prothallial cell and a generative cell, each invested by a thin membrane (Text-fig. 42). This stage represents the microspore at the period of dehiscence and dispersal, and is the phase characteristic of the numerous microspores present in the young pollen-chamber (Text-fig. 38). This cavity has been formed by the breaking down of cells in the beaked part of the nucellus which protrudes into the micropyle (Text-fig. 20).

Pollination.

During November the wind-borne microspores drift down between the megasporophylls which, at this period, have become slightly separated by elongation of the cone axis. At such time, too, the significant observation was made that a tiny drop of fluid appears at the end of each micropyle, as has been explained by Webber (1901) and Chamberlain (1935). The microspores adhere to this liquid which, by its subsequent evaporation, draws the pollen grains down the micropyle to be lodged in the young pollen chamber (Text-fig. 38). The cells, which have broken down to form this chamber, may furnish the liquid referred to. In a single longitudinal section of a pollen chamber (Text-fig. 38) eleven microspores are in view, so that the total number in the complete chamber must be very considerably more.

Baird (1939), in the case of *Macrozamia Reidlei,* is convinced that insects play "an important part in transferring pollen from the cracks between the megasporophylls to the micropyle". During the collection of material of *Macrozamia spiralis* the writers made frequent observations regarding this point, and reached the conclusion that although insects, chiefly beetles, may be encountered amongst the younger vegetative leaves, and even among the sporophylls of both kinds of cones, yet their presence is fortuitous and sporadic.

Furthermore, while pollen which has already been carried by the wind to the ovulate cones may on occasion be transferred by insects from a megasporophyll to the micropyle of an ovule, yet such a rare happening is not to be regarded as of any real significance in the mechanism of pollination which, for all practical purposes, is anemophilous.

Text-fig. 39.—Optical section of a microspore removed from a microsporangium prior to dehiscence. The exine and intine and large central nucleus are indicated. 12 Nov., 1938. × 960.

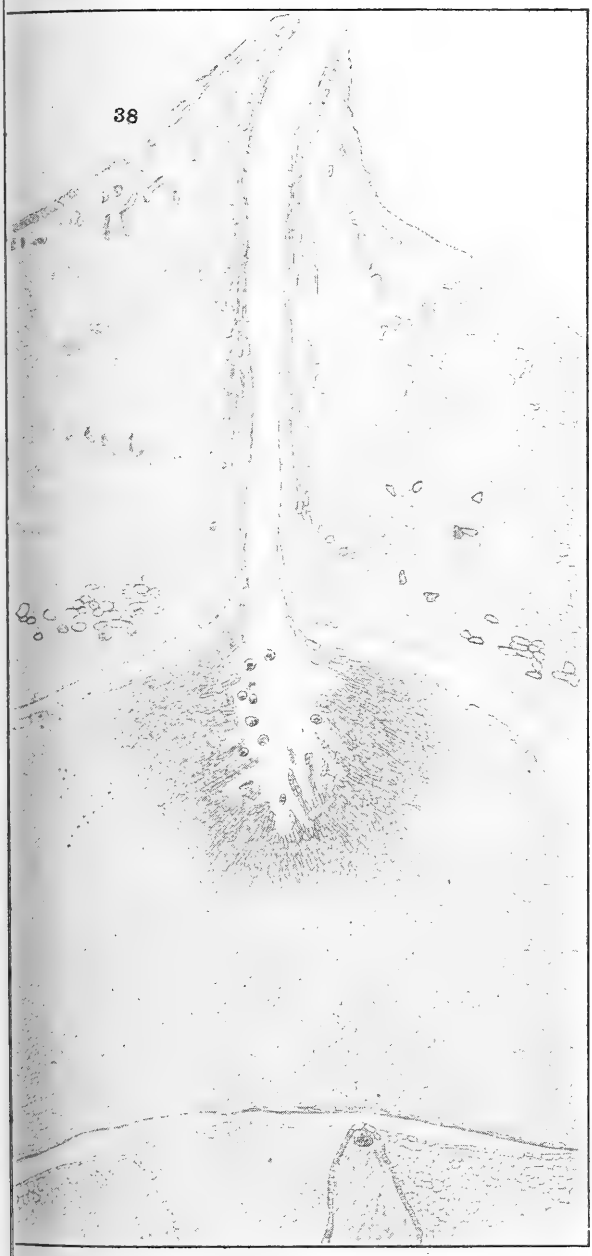
Text-figs. 40, 41.—Sections from material slightly older than that of preceding figure. The single nucleus has divided to produce two nuclei. One, surrounded by cytoplasm and a thin wall, lies against the wall of the spore and represents the prothallial cell, while the other, a spherical nucleus, occupies a central position. Some starch grains are present in the cytoplasm. 12 Nov., 1938. × 960.

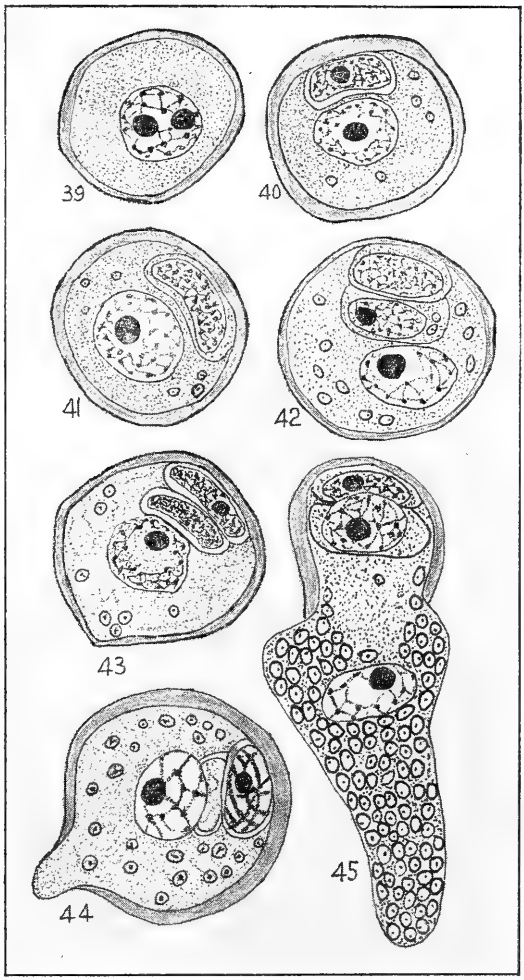
Text-fig. 42.—Transverse section of microspore at shedding stage. The central nucleus has divided, giving rise to a central generative nucleus and tube-nucleus. Starch grains have become more numerous. 12 Nov., 1938. × 960.

Text-fig. 43.—Section of pollen grain within pollen chamber, just after pollination of ovule. The slight swelling on one side indicates the commencement of growth of the pollen tube. 12 Nov., 1938. × 960.

Text-fig. 44.—Section of microspore and developing male gametophyte: the intine has ruptured the thinner region of the exine and protrudes as a blunt tube; the starch content has steadily increased. 12 Nov., 1938. × 960.

Text-fig. 45.—A later stage of the male gametophyte showing further development of the pollen tube, especially in breadth; the tube-nucleus has moved into the tube which is densely packed with starch grains.



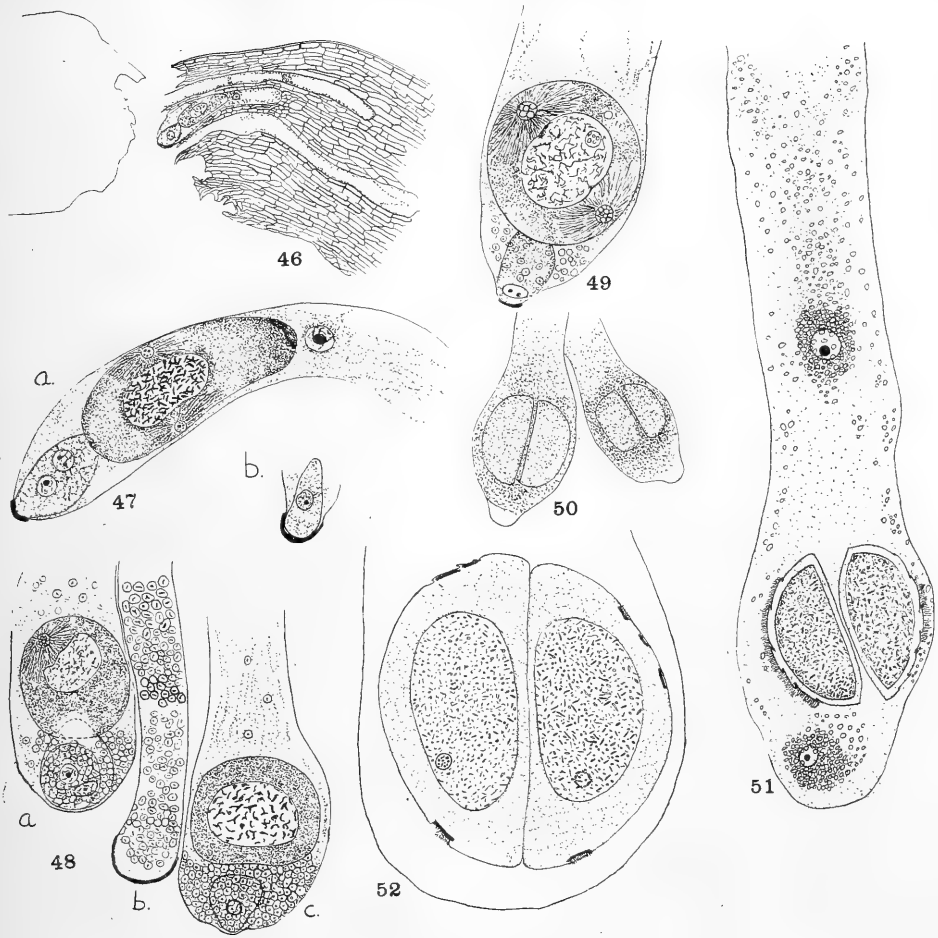


Text-fig. 38.—Median longitudinal section of the upper portion of an ovule during pollination stage. The thick integument contains numerous mucilage ducts, and tannin cells, and is prolonged into a low beak enclosing a long narrow micropyle, which is funnel-shaped at the apex, and lined internally by a definite layer of relatively small secretory epidermal cells. The long, narrow, hardened nucellar beak projects a considerable distance into the micropyle. The cells of the central region of this beak have distintegrated to form the apical narrow passage which lower down expands into the enlarging pollen chamber in which numerous pollen grains at the 3-nucleate stage of the gametophyte are evident.

Below this again is a deep zone of nucellar tissue which caps the female gametophyte, in which are seen portions of two archegonia with young neck-cells and a large central cell with highly vacuolate contents. 12 Nov., 1938. × 40.

The Late Male Gametophyte.

Further development of the male gametophyte may proceed without any interval of rest, but at any time various stages can be seen in any pollen chamber inspected. Growth is marked by the greater number of starch grains, a small increase in the size of the spores, and protrusion of the intine (Text-figs. 43 and 44) to initiate the pollen tube. A slightly older stage is illustrated in Text-figure 45, in which it is evident that the tube-nucleus has entered the pollen tube, the tip of which has invaded the nucellar tissue approximately at right angles to the long axis of the pollen chamber. As the tube elongates, the position taken by the tube-nucleus is not fixed, but may be anywhere from almost touching the body cell (Text-figs. 46 and 47) to close proximity to the end penetrating the tissue. The latter is the usual location in the final stages of development. As growth proceeds the haustorial portions of the pollen tubes may branch a few times (Text-figs. 53 and 56) so that the nucellar cap becomes completely riddled, the component cells deprived of their contents, and eventually represented by a flattened mass of collapsed cell walls. By this means the pollen tube is well nourished, and that the process is efficient appears from the dense aggregation of starch grains particularly in that region of the gametophyte adjoining the pollen chamber, where marked activity is evident. Division of the nucleus in this region has resulted in the formation of the prothallial cell and the generative cell, which latter, in turn, divides to give the stalk-cell and the body-cell. During this phase the aggregation of starch—which is particularly well defined by Newton's method of staining—is so marked that considerable difficulty may be experienced in following the successive changes, and the limits of the cells concerned. This difficulty is increased by the frequent overlapping of the cells under observation, namely, the prothallial cell, stalk-cell and the body-cell. However, as is indicated in Text-figures 48 (*a*, *b* and *c*), it was established that the prothallial cell and the stalk-cell occupy the tip of the tube which is in part still encased in the exine. The stalk-cell may extend upwards beyond the lower limit of the body-cell. In so doing it, when fully developed, presses into the latter without, however, rupturing the impinging walls concerned (Text-figs. 47*a*, 48*a* and 49). At maturity the prothallial cell has a distinct nucleus, is somewhat elongated, and in shape varies from elliptical to pyriform with the narrower end towards the body-cell (Text-fig. 47*b*). The latter rapidly increases in size and bears a strikingly large nucleus with dense contents. Very soon two blepharoplasts, disposed at opposite poles, become apparent. Each contains several vacuoles which impart a granular appearance to the organ. With each blepharoplast radiating fibrils of cytoplasm become early associated (Text-figs. 47*a* and 49) and eventually the characteristic appearance of the mature body-cell is attained. The orientation of the blepharoplasts is usually in the long axis of the tube, but may be inclined, or even at right angles, as is seen in Text-figure 47*a*, where it has been forced to assume a flattened form owing to the restrictions imposed by the configuration of this particular pollen tube. Meanwhile, the proximal regions of the tubes, densely packed with starch grains, have elongated, increased in diameter, and now hang vertically downward with their tips protruding into the archegonial chamber. A score, or even more, of these tubes may be seen in a single chamber, but the average number is about a dozen. Text-figures 54, 55, 56 and 57 show the nucellar cap with numerous pendent pollen tubes. Ultimately the body-cell becomes orientated so that a line joining the blepharoplasts lies at right angles to the long axis of the pollen tube (Text-fig. 49). The nucleus of the body-cell is very large and rich in chromatin (Text-fig. 48, *a* and *b*), while the blepharoplasts, each with its conspicuous radiating fibrils of cytoplasm, are especially prominent structural features of the cell. Division of the body-cell, which occurs early in January, gives rise to two mother cells, each containing a sperm with spirally arranged ciliated band so characteristic of cycads (Text-fig. 58). The processes leading to the production of such sperms show no unusual features, and have been so often and so fully described that little purpose would be served in recapitulating the successive phases. Pollen tubes dissected from living



Text-fig. 46.—Median vertical section through nucellus showing, on right, the haustorial nature of the vacuolate pollen tubes. The centrally-placed gametophyte shows the stalk cell, body cell and tube-nucleus. 31 Dec., 1938. × 40.

Text-fig. 47.—(*a*) Median longitudinal section of the generative region of an immature male gametophyte. The remains of the exine are still evident, and adjoining is the stalk cell, which conceals the smaller prothallial cell except for the nucleus. Next is the flattened body-cell with its large nucleus and two conspicuous polar blepharoplasts, while beyond is the tube-nucleus. The small supplementary diagram (*b*) shows outline of the prothallial cell, seen in a different plane. 31 Dec., 1938. × 140.

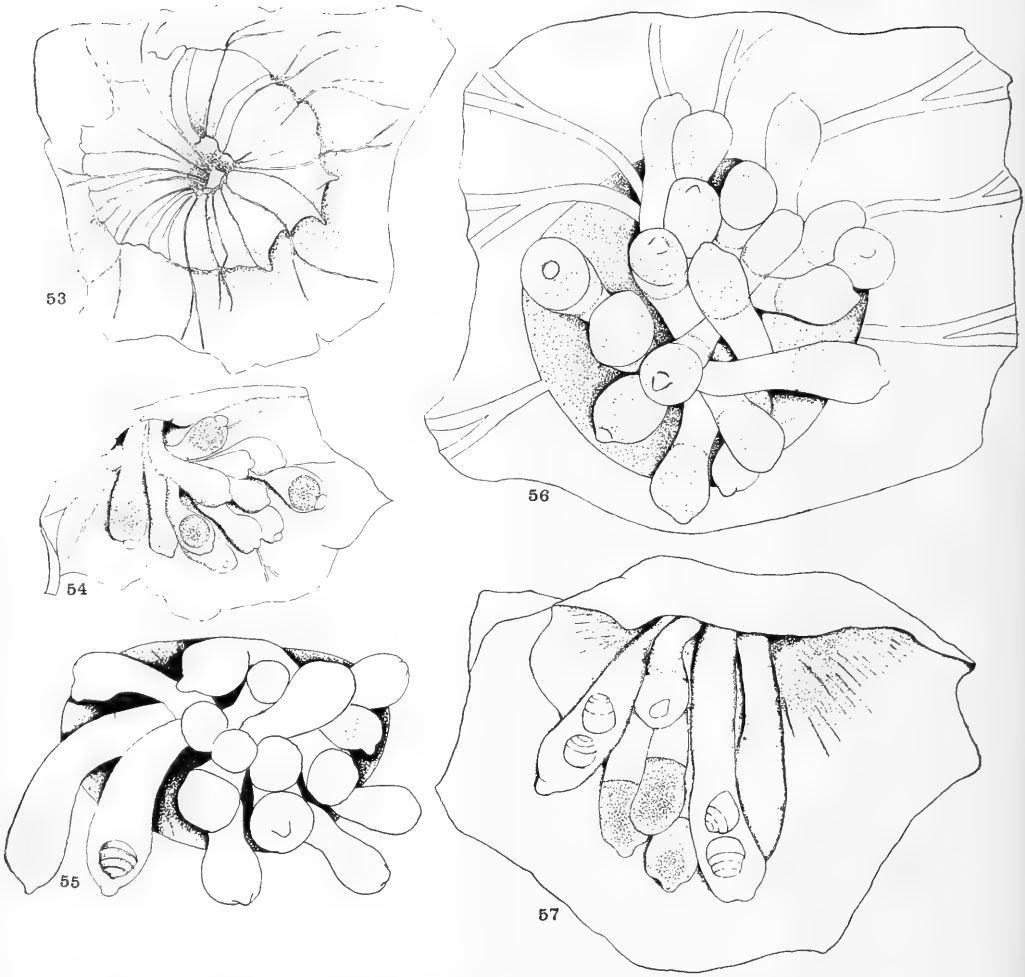
Text-fig. 48.—The generative tips of three male gametophytes in longitudinal section. In (*a*) may be seen the prothallial cell, the upper part of which overlaps the lower region of the body cell where the nucleus and one of the blepharoplasts are visible. The tip of the pollen tube is crammed with starch grains which tend to cloak the contents; (*b*) is not median but illustrates the abundant starch and portion of exine, while (*c*) shows the prothallial and body cells. 12 Nov., 1938. × 140.

Text-fig. 49.—This figure shows again the generative tip of gametophyte with the prothallial cell projecting beyond and behind the body cell, the latter possessing two blepharoplasts with radiating fibres and a prominent nucleus with a large nucleolus. 31 Dec., 1938. × 140.

Text-fig. 50.—This represents the tips of two male gametophytes pendent from the nucellar cap. The body cell has divided to give two sperm cells. The papillae, which are the remains of the exine, are very prominent at the apices of the tubes. 29 Jan., 1939. × 29.

Text-fig. 51.—Part of a pollen tube exposed in a longitudinal section of the nucellar cap It shows the tube-nucleus surrounded by an aggregation of starch grains, the two sperm cells towards the free end, each with a much enlarged nucleus, portions of the developing spiral band in section, and at tip, the prothallial nucleus also amid starch grains. 21 Jan., 1939. × 116.

Text-fig. 52.—Longitudinal section of tip of the generative region of male gametophyte showing the two large immature sperm cells. The series of furrows caused by the spiral band are obvious in the wall and from these deeply-staining tufts of short cilia project. 10 Jan., 1939. × 268.



Text-fig. 53.—Dorsal view of part of the apical region of the nucellar cap. In the centre is the pollen chamber and radiating therefrom a series of long, branching haustorial tubes of male gametophytes, permeating the tissue of the nucellus. The central region of the nucellus is typically cone-like with a crater-like opening in the middle. Drawn with a binocular microscope from living specimen. 31 Dec., 1938. × 24.

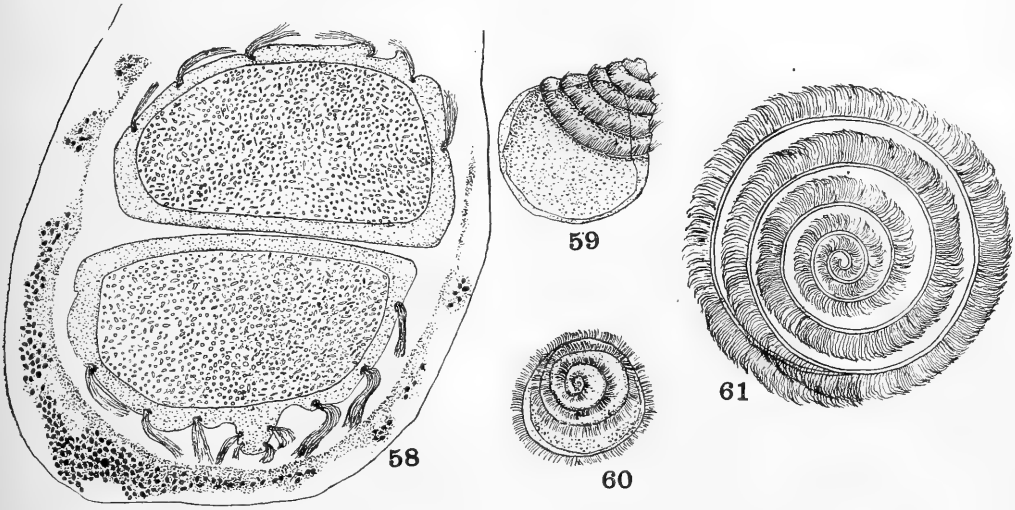
Text-fig. 54.—Ventral view of the nucellar cap described in previous figure. The lateral gametophytic haustoria can be seen through the thin nucellus whilst pendent in the centre are the generative ends of the pollen tubes. These are dilated, club-shaped structures projecting in close formation beyond the narrow passage of the broken-down pollen chamber, and protruding slightly into the archegonial chamber. Each shows a small papilla-like projection at the tip, which marks the position of the original microspore. The contents are indistinct, but the motile sperm stage has not been reached. 10 Jan., 1939. × 20.

Text-fig. 55.—A stage slightly more advanced than that depicted in preceding figure. In one tube motile sperms were seen, but the majority of the others had shed their sperms and were devoid of contents. 10 Jan., 1939. × 24.

Text-fig. 56.—Another view of the ventral surface of the nucellus with the generative regions of upwards of a score of pollen tubes now extended deeply into the archegonial chamber. The nucellus is greatly attenuated, its substance having been absorbed by the haustoria. A body-cell is located near the protruding tip of each tube. 21 Jan., 1939. × 24.

Text-fig. 57.—Side view of a nucellar cap similar to those illustrated in preceding figures. It shows to better advantage the depth to which the sperm-bearing ends of the pollen tubes hang below the surface of the nucellus after penetrating the pollen chamber. Sperms are present near tips of tubes. Drawn from living material with binocular microscope. 31 Jan., 1939. × 24.

material in the third week of January, and examined under the binocular microscope, presented the arresting spectacle of the active sperms swimming upward and downward in the liquid contained in the pendent region of the tube. The sperms moved forward, and at the same time each rotated on its axis. While under observation they retained their activity for varying periods up to ten minutes (Text-figs. 55 and 57). Drawings made after the quiescent stage had been reached are shown in Text-figures 59 and 60. The appearance of a living sperm with five coils in its ciliated band is portrayed, while a



Text-fig. 58.—Longitudinal section of generative tip of pollen tube containing two sperm cells, almost mature. The furrows caused by the spiral band are now very deep, and the long densely-arranged cilia project freely. Abundant starch grains are embedded in the surrounding cytoplasm. 21 Jan., 1939. × 365.

Text-fig. 59.—Lateral view of a living sperm. Its pyramidal shape and spiral ciliated band are obvious. This sperm was forced out of the pollen tube and for a short time swam freely in the liquid exuded. The huge nucleus is almost spherical. Drawn with binocular microscope. 31 Jan., 1939. × 75.

Text-fig. 60.—Surface view of a living sperm. The symmetrical coiling of the spiral band which executes five complete turns is remarkably clear. The closely set cilia vibrate with great rapidity. Drawn with binocular microscope. 31 Jan., 1939. × 75.

Text-fig. 61.—A high-power study of a sperm in surface view. This illustrates the length of the cilia and their arrangement on the spirally-coiled band. 21 Jan., 1939. × 235.

surface view from a stained preparation is depicted in Text-figure 61. The appearance of the young sperms in section, soon after their formation, each with its large nucleus and spiral ciliated band, is indicated in Text-figure 52, while the general contents of the pollen tube, namely, starch grains, tube-nucleus, mature sperms and stalk-cell nucleus, are featured in the text-figure immediately preceding. The structure of the mature sperms, now free from each other, is better illustrated in Text-figure 58, where the grooves due to the pressure of the ciliated band are more pronounced. As already stated, pollination occurs normally during the latter half of October and early November, while fertilization is not effected until mid-January, so that a period of a little over two months elapses between these two significant events.

Fertilization.

The thin nucellar cap fits over the archegonial chamber, forming a compartment sealed off from the outer air (Text-figs. 38 and 53). Pollen tubes removed from this chamber, and exposed to the external atmosphere with a high relative humidity and a temperature of 80° Fahrenheit, showed immediate symptoms of desiccation, thereby indicating that the moisture content of the internal atmosphere must be saturated. In support of this theory it was noted that the walls of the chamber were moist. It follows, therefore, that in more mature ovules, where the contents of the pollen tubes have been

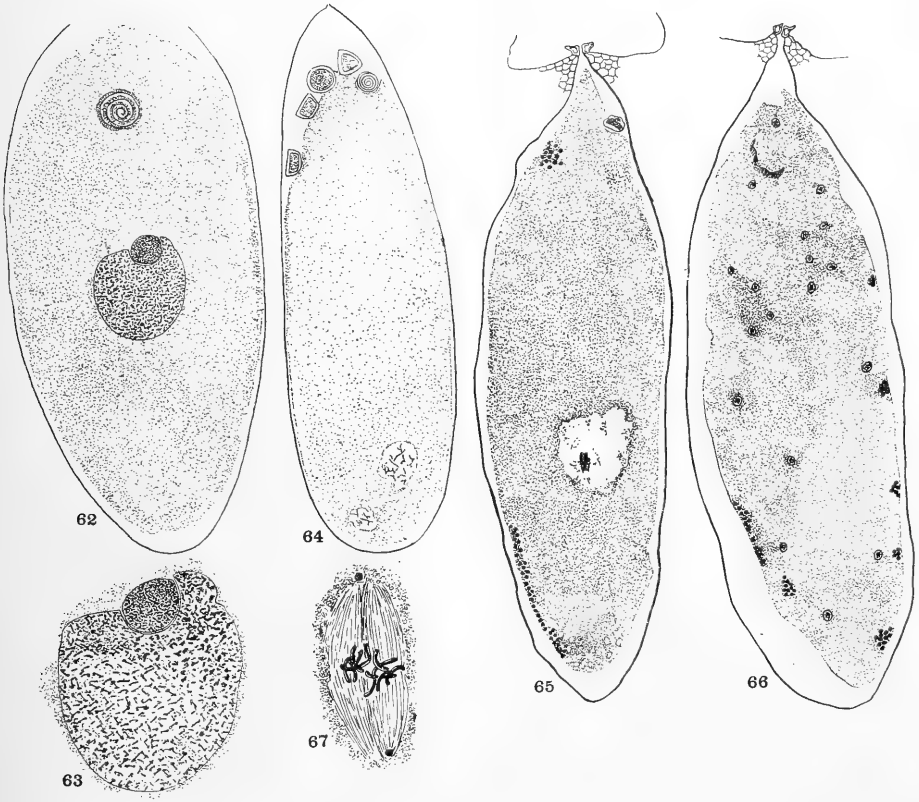
ejected into such an environment, there is little chance of desiccation of the sperms even though their passage through the neck cells into the egg be not immediately effected. The quantity of this fluid must be considerable, seeing that as many as twenty pollen tubes may discharge into one chamber, and in consequence provide sufficient liquid to submerge the exceptionally large sperms. Lawson (1926) contends that the neck-cells "actually secrete water after the manner of superficial hydathodes", and that the sperms can and do swim within the archegonial chamber. It may be pointed out, however, that the amount of free water secreted could not be very large, otherwise it would dilute the liquid ejected from the pollen tubes, and thus by osmosis increase the internal pressure of the sperms to a harmful extent. The neck-cells are a conspicuous feature of the mature archegonium (Text-figs. 32 and 33). The writers have not found in *Macrozamia* the differential thickening of the walls of the neck-cells which Lawson figures in *Bowenia*, and if this particular structural feature is a necessary condition to his explanation of the opening mechanism for the passage of sperms, such a method is inoperative in *Macrozamia*. In Text-figure 32, it may be seen that the part of the adjoining walls actually in contact at the period just prior to fertilization is limited. Accordingly, it is easily conceivable that at the precise period when sperms are free in the archegonial chamber, very little modification in the shape of the neck-cells —owing to some change in their turgidity—in conjunction with the upward thrust of the extremely turgid contents of the egg would lead to their actual separation. Even though this passage be less than 215μ (the average diameter of the sperm), an entry may be effected either by the slight force exerted by the sperm or by modification in its shape, since such fluctuation in form has already been noted while the sperm was still swimming in the pollen tube. No matter what the correct explanation may be, the fact remains that the mechanism is most efficient, since in many cases several sperms gain entry to a single egg.

Considering that a score of pollen tubes and five archegonia are not uncommon in one chamber, that is, a ratio of eight sperms to each egg, it is not surprising that numerous sperms may enter any one egg. In Text-figure 64 five sperms, in addition to the functional one, have passed through the neck-cells. These superfluous sperms degenerate but slowly, and are easily recognizable even in the early stages of development of the embryo, albeit the cilia are no longer apparent. The neck-cells appear to be unaltered by the entry of these sperms, since examination at the post-fertilization stage showed no malformation. The functional sperm escapes from its sheath which is left in cytoplasm near the periphery of the egg, the ciliated band being an easily recognizable feature, however, until wall-formation in the proembryo. The male nucleus gradually moves towards the egg nucleus with which it finally makes contact, their membranes, however, remaining intact. The disparity in size of the two nuclei is striking (Text-fig. 62). Each contains a large amount of a deeply-staining substance which, as Chamberlain (1935) points out, has never been satisfactorily interpreted, and this constitutes the "metaplasm" of Strasburger. Even at the stage when the male nucleus has become practically engulfed in the egg nucleus, nothing which could be diagnosed as chromatin was observed (Text-fig. 63).

The Embryo.

After fertilization, during which contact of the sperm and egg and the subsequent union of their nuclei have resulted in the formation of the zygote, development proceeds rapidly. The earliest clearly recognized stage in embryogeny was the metaphase of the nuclear division of the zygote (Text-fig. 65). The spindle takes the position formerly occupied by the nucleus of the egg, that is, just within the lower half of the egg-sac, and is surrounded by a large clear region, referred to by Chamberlain (1935) as the "fibrillar area", and containing a few widely separated cytoplasmic strands somewhat akin to spindle fibres. The number of chromosomes identified during a study of consecutive sections through two different spindles of the dividing zygote nucleus conforms with the number eighteen ascertained for *Macrozamia Miquelii*, *Macrozamia Moorei* and *Macrozamia tridentata* by Sax and Beale (1934). The double structure of the fusion spindle described by Lawson (1926) for *Bowenia* was not positively identified in

the present case, but the rather broad blunt-ended spindle of this first division does suggest a dual nature (Text-fig. 67). However, later stages fail to show the double spindle which Lawson states persists "up to the last mitosis forming free nuclei in the proembryo". Sections through the proembryo of *Macrozamia spiralis* show that



Text-fig. 62.—A longitudinal section through an archegonium during the period of fertilization. The actual fusion of the sperm nucleus with that of the egg is depicted. The membrane of each nucleus is still intact, the ciliated spiral band of the male nucleus being left behind in the upper cytoplasm at the time when the nucleus escaped from its sheath. The cytoplasm is contracted from the apical region of the egg, leaving a hyaline region filled with liquid. 21 Jan., 1939. × 28.

Text-fig. 63.—High-power study of the union of the male and female nuclei; the former is almost entirely enveloped in the metaplasm of the egg nucleus. The contents of the sperm nucleus are finely granular, while those of the egg are exceedingly coarse in comparison. 21 Jan., 1939. × 58.

Text-fig. 64.—Longitudinal section of an egg. Five sperms have effected an entrance and impinge on the egg cytoplasm, between the margin of which and the apex is the characteristic hyaline region. One of the sperms with its ciliated band is partly buried in the cytoplasm but the others, which stain more deeply, appear to be degenerating. At the lower end of the egg two protein vacuoles occur but the egg-nucleus is not included in this section. 21 Jan., 1939. × 28.

Text-fig. 65.—Median longitudinal section through an archegonium soon after fertilization, showing the metaphase spindle of the division of the zygote nucleus. It is surrounded by a clear fibrillar zone; also in evidence are an accumulation of starch grains towards base of egg, the collapsed neck-cells, an intact egg-sac membrane and a non-functional sperm impinging on the upper cytoplasm. 29 Jan., 1939. × 33.

Text-fig. 66.—Early nuclear division in the proembryo showing a number of intranuclear spindles, scattered generally throughout the granular cytoplasm; the remains of the ciliated band of the functional sperm are embedded in the upper cytoplasm. 29 Jan., 1939. × 33.

Text-fig. 67.—Highly magnified view of spindle of previous figure showing some of the chromosomes, also the blunt ends and suggestion of dual nature of the spindle. 29 Jan., 1939. × 355.

simultaneous divisions of the nuclei do occur, and that a number of free nuclei are distributed uniformly throughout the cytoplasm (Text-fig. 66). Such divisions are intra-nuclear, the membrane being a conspicuous feature until very late stages in free nuclear division. In the upper cytoplasm, the discarded, coiled, spiral sheath of the functional sperm still persists, and even the fine cilia are distinctly visible. By this time the archegonial neck-cells have collapsed, but the egg membrane has thickened very considerably and forms a clearly delineated boundary to the developing proembryo. So far, uniform distribution of the nuclei has been maintained, but on reaching the 128-nucleate stage there is a definite tendency for the majority of the nuclei to segregate at the lower end of the proembryo. The abundance of starch grains in this region may indicate a general "settling", as pointed out by Coulter and Chamberlain (1903) in the case of *Zamia*, but no definite cytoplasmic strands were diagnosed (Text-fig. 68).

It is probable, too, that in the lower region subsequent divisions of the nuclei proceed more rapidly: certainly wall formation is initiated here earlier than in the upper part. Wall formation commences with the development of a peripheral layer of cells and a centripetal growth of the tissue thus initiated (Text-fig. 69). Again, development proceeds more rapidly at the lower end. No sign of the formation of evanescent walls prior to true wall formation, such as has been observed for *Dioon* and *Stangeria* (Chamberlain, 1935), was observed in the case of *Macrozamia spiralis*. After the free nuclear stage the proembryo becomes cellular throughout and in this respect agrees with "some species of *Cycas*, *Encephalartos*, and *Macrozamia*" (Chamberlain, 1935), but differs from *Macrozamia Reidlei* (Baird, 1939) in which there is "a small region in the centre, which remains non-cellular with free nuclei" and which "breaks down about the time the embryo is beginning to differentiate". Furthermore, in the embryogeny of *Macrozamia spiralis* the completely cellular condition once attained is a persistent feature, and at no subsequent stage is there in the central region that breaking-down of tissue which is so characteristic of those other cycads in which the early proembryo is recorded as being cellular throughout. Subsequent development leads to increase in size of the proembryo, but growth continues to be more vigorous at the lower end, where a mass of small densely cytoplasmic cells become segregated (Text-fig. 70). The cells of this region are in marked contrast to the larger vacuolate cells of the rest of the proembryo.

The next phase of importance is marked by the elongation of the cells comprising the four or five tiers immediately behind the actively meristematic zone (Text-fig. 71). The young suspensor, thus initiated, grows rapidly, particularly in length, so that the embryonic apex is forced downwards, eventually ruptures the tough egg-membrane (Text-fig. 72 and 73), and makes direct contact with the endosperm. Thereupon, enzyme action (Pl. xvii, fig. 23) results in the provision of an abundant food supply for the nourishment of a massive embryo (Text-fig. 73).

Elongation of the suspensor, however, greatly exceeds the actual distance penetrated into the endosperm. Consequently, the suspensor becomes coiled and twisted. It finds

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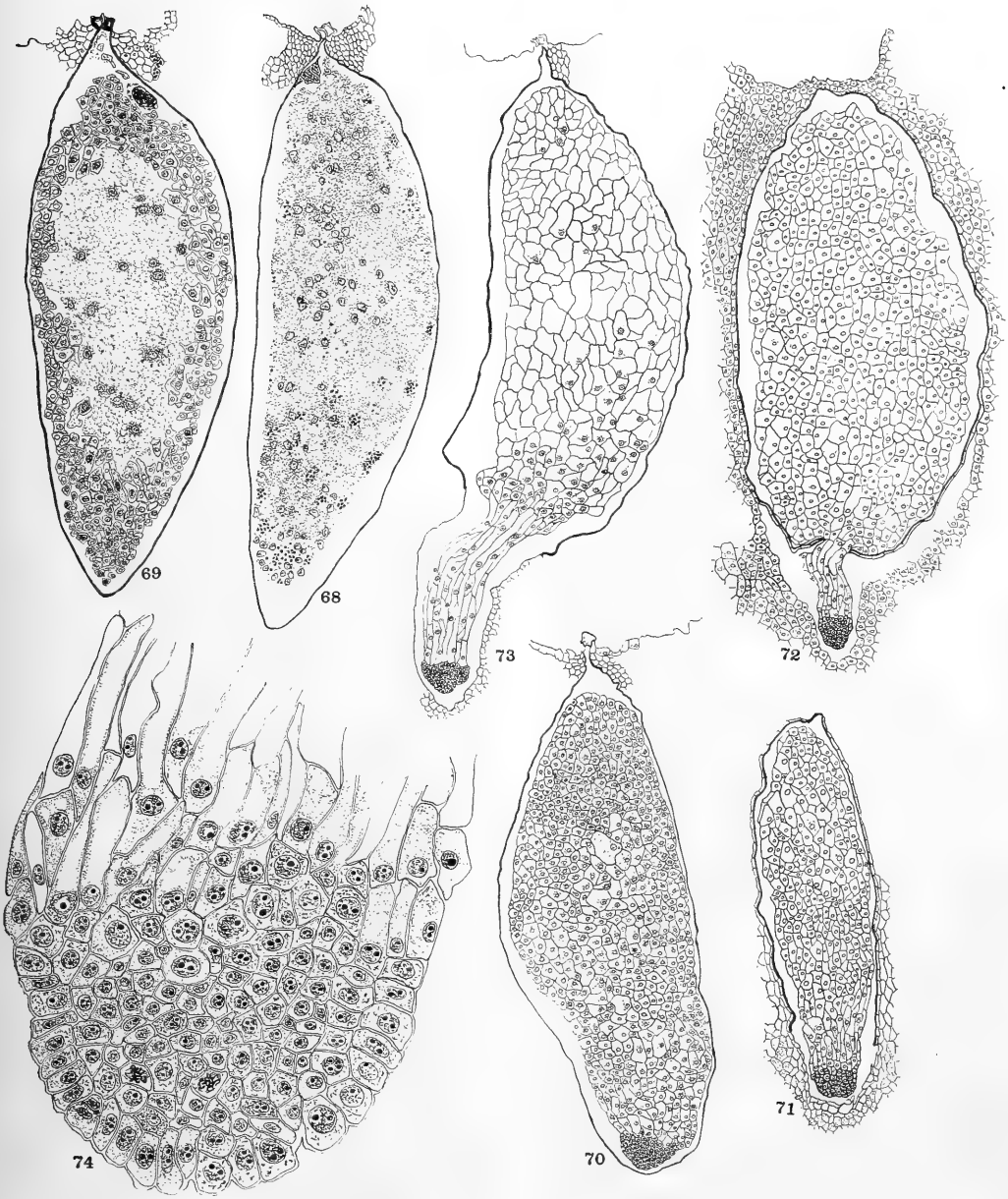
Text-fig. 71.—In this longitudinal section, which is not quite median, differentiation of the suspensor cells has been initiated, the cells immediately behind the meristematic zone showing vacuolation and elongation. The general increase in length of the proembryo has caused the sac membrane to rupture in the region adjacent to the meristem. 2 March, 1939. × 22.

Text-fig. 72.—A still older stage of the proembryo; the suspensor is clearly established, and has thrust the embryo through the membrane and into the endosperm tissue. 5 March, 1939. × 33.

Text-fig. 73.—A representation of a still older stage in the development of the proembryo. The suspensor cells have increased greatly in length and the embryo proper has been forced deep into the tissue of the endosperm. The surrounding clear zone is due to enzyme secretion by the embryo with consequent digestion of the contiguous cells. 5 March, 1939. × 33.

Text-fig. 74.—High-power representation of a longitudinal section of the lower part of a young suspensor, and terminal meristem. The cells of the latter are densely cytoplasmic, and their meristematic activity is attested by the numerous nuclei undergoing division. 5 March, 1939. × 355.



Text-fig. 68.—Stage of development of proembryo somewhat later than that portrayed in Text-figure 66. Further nuclear divisions have occurred, and about ninety-six nuclei are now visible in the cytoplasm of the proembryo. These nuclei tend to congregate at the base of the sac, while the amount of starch has increased, especially at the lower end. The membrane of the sac is still intact and a non-functional sperm lies within the collapsed neck-cells at the upper end. 31 Jan., 1939. × 33.

Text-fig. 69.—This longitudinal section through the developing proembryo shows the initiation of true cell-walls. Around the periphery the cells are smaller and more crowded towards the lower region. Numerous free nuclei embedded in cytoplasm still occupy the central region. 31 Jan., 1939. × 33.

Text-fig. 70.—Median longitudinal section of young proembryo which has now become completely cellular. The differentiation of a meristematic zone at the base of the sac is evident, while larger vacuolate cells occupy the central and upper parts. 5 March, 1939. × 33.

accommodation for an increasing bulk by breaking down the cells and filling the space formerly occupied by the relatively extensive and soft tissue of the upper region of the proembryo. All the eggs of a female gametophyte may be fertilized, and any or all of the resulting zygotes may develop vigorously (Text-fig. 80). Consequently a young seed usually contains an endosperm into which several embryos with long suspensors have burrowed. So long as these suspensors are fairly straight the embryos concerned may easily be dissected one from another (Pl. xvii, figs. 21 and 22), but subsequent elongation and coiling in a restricted space results in the suspensors becoming inextricably intermingled within the common cavity formed from the space formerly occupied by the egg and the partial disintegration of the endosperm (Pl. xvii, figs. 19 and 20).

At this point it is interesting to observe that the several tough egg-membranes still persist in the seed, and may be recognized as balloon-like structures, each enclosing the upper portion of a young sporophyte (Text-fig. 80). Of course, such membranes are later crushed by the enlarging embryos. Lawson (1926), in describing the embryology of *Bowenia*, has stated that the suspensors may fuse together at different points. The present investigation does not support the idea of anything in the nature of organic union but rather that, as Chamberlain (1935) has explained, they are intimately associated and form a composite body until, during later development, one embryo after another ceases growth, and is left behind until only one survives. The suspensor of this embryo, however, persists, and may reach at maturity a length, when extended, of 9·5 centimetres (Text-fig. 83), by which time all the primary organs of the embryo have been differentiated. But in *Macrozamia spiralis* a more novel and interesting method of increasing the number of embryos in any one seed has been observed. The condition has been attained through budding of the embryo, so that another kind of polyembryony arises. It originates in a manner totally different from that described above for *Macrozamia spiralis* in particular, and for cycads in general. Dissection, and examination of sections, of young seeds showed that several embryos may arise within a single egg-membrane. For example, in a single seed collected during February, when the embryos are still sufficiently young to be easily separated, five out of the six embryos from different archegonia possessed either two or three meristems. In three of the cases the lateral meristems were far removed from the basal meristematic zone (Text-figs. 77, 78 and 79), but in one case two growing points, located side by side, occupied the lower extremity of the embryo (Text-fig. 76). Some of these embryos had already developed short suspensors. Baird (1939) has drawn attention to the occurrence of such embryos in *Macrozamia Reidlei*.

Reference to Text-figures 75 to 79 shows where and how such supernumerary individuals arise. It is clear that the superficial cells in any region of the proembryo—except perhaps that portion adjoining the neck-cells—may become meristematic, and that the actively dividing zones thus formed rapidly develop the essential features of the normal embryo. Such embryos grow out in all directions and eventually impinge on, and penetrate, the egg-membrane. In some cases the direction of further growth is deflected by resistance of the tough membrane, and then the tips usually turn downwards in the direction of the rupture effected by the first-formed and normal embryo. Some embryos, however, are deflected in an upward direction and provide the striking spectacle of young sporophytes growing in the direction of the micropyle. However, none of the inverted embryos observed developed sufficiently to permit of their passing beyond the limits of the archegonium.

Branching of the suspensor has been recorded in *Encephalartos* by Saxton (1910). In the present investigation two well-developed embryos of approximately the same

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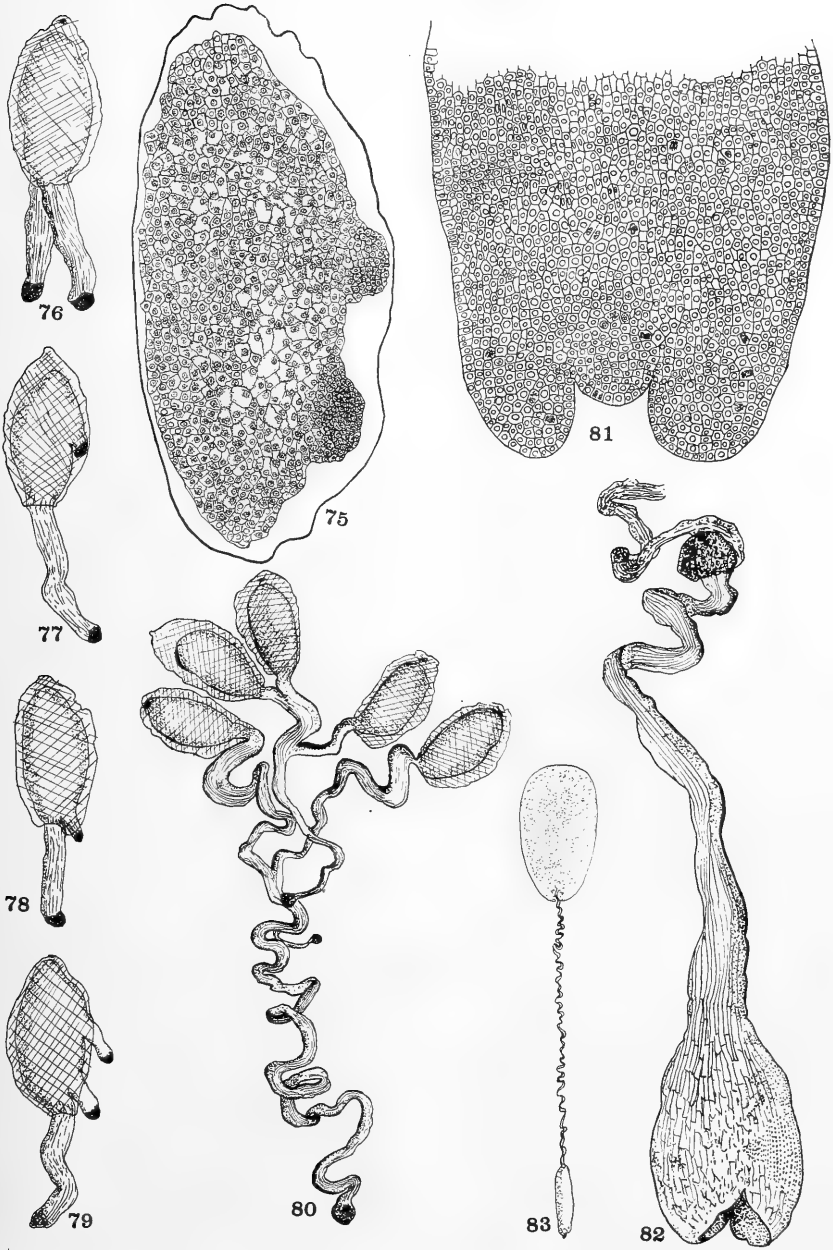
Text-fig. 81.—Median longitudinal section of early cotyledon stage of the embryo; the stem tip is terminal and the two cotyledons lateral. 11 March, 1938. × 96.

Text-fig. 82.—A slightly older embryo than that depicted in previous figure. Two broad fleshy cotyledons are evident. The region behind the cotyledons gives rise to the coleorhiza. 12 May, 1939. × 8·4.

Text-fig. 83.—A megascopic view of endosperm of a seed dissected to show the extent of the coiled suspensor and the large embryo proper attached. 7 June, 1939. × 0·4.



Text-fig. 75.—This diagram shows a longitudinal section through a proembryo, possessing lateral meristems as well as a normal basal meristem; the latter is not included in this drawing but was observed in succeeding sections of the series. In no case have suspensor cells been initiated. 5 March, 1939. × 40.

Text-figs. 76 to 79.—Diagrams 76 to 79 illustrate polyembryony due to sporophytic budding, and embody a series of proembryos dissected from a single seed. In figure 76 a lateral embryo is seen alongside the terminal one; in figure 77 the relatively undeveloped lateral embryo is still within the egg membrane; in figure 78 a lateral embryo has penetrated the egg membrane, while the succeeding figure depicts a proembryo with two lateral individuals originating at different levels. In all cases a suspensor has been developed, but these vary considerably in length. 18 Feb., 1940. × 7·2.

Text-fig. 80.—This diagram illustrates five embryos derived from five different archegonia. The coiled suspensors are closely intertwined, and all but one of the embryos have aborted. The persistent egg membranes are conspicuous. 13 April, 1939. × 3·6.

dimensions were occasionally found in the position usually occupied by the normal embryo, an occurrence which naturally suggested an origin identical with that claimed in *Encephalartos*. However, the study of suitable material at earlier stages showed that a secondary meristematic zone may be found close to, and very soon after, the inception of the first-formed apical meristematic tip. In this case, seeing that no suspensor has yet been developed, branching of the suspensor as the cause of polyembryony is clearly excluded, and in *Macrozamia* no evidence of such a happening has so far come to light. The known facts indicate that embryos arise independently from the undifferentiated proembryo, although the possibility of increase by division of the apical meristem itself is not precluded.

As already indicated the budded embryos abort relatively early and, in seeds containing an advanced embryo, no trace of their presence was discovered.

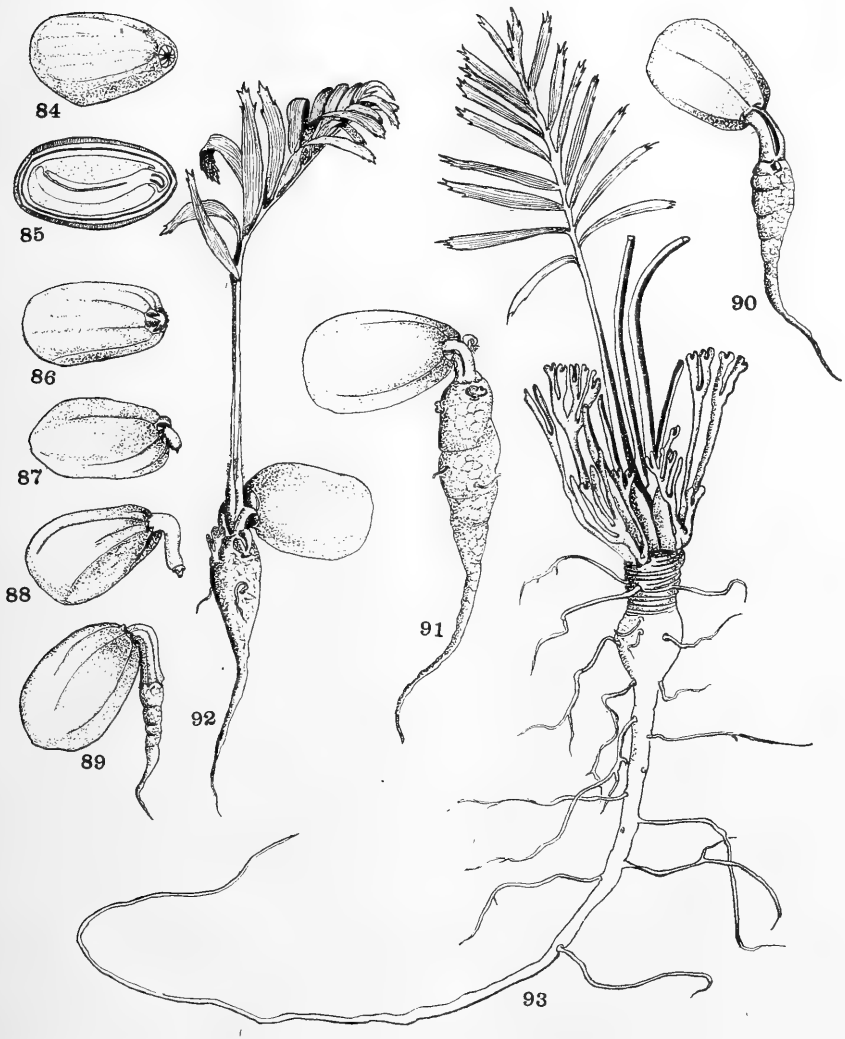
Eventually, all but one of the embryos which may have commenced development in any one seed become crushed and absorbed by the functional one which slowly but steadily invades the endosperm and increases in size. Microtome sections of the endosperm of seeds collected in March showed the epicotyl and the primordia of the two cotyledons (Text-fig. 81). The latter grow rapidly until in May they appear as relatively large, fleshy organs as represented in Text-figure 82.

By late June the epicotyl, cotyledons, hypocotyl and root of the embryo are recognizable. Thereafter a steady increase in size of the various parts proceeds until material examined in December reveals an embryo about 2·3 centimetres in length attached to a suspensor which, even when slightly coiled, extends to a length of 9 centimetres (Text-fig. 83).

Germination and the Seedling.

Subsequent to fertilization the axis of the cone slowly elongates. Thereby the megasporophylls are separated, the seeds become exposed, and are conspicuous on account of their vivid colour which in different cones varies from yellow to pink or deep red. Meanwhile a gradual process of desiccation is operative, and the formation of an abscission layer near the base of each sporophyll eventually leads to its falling away from the cone axis, and the deposition of a colourful mass of seeds around the bare and protruding peduncle. Such seeds gradually become freed from the sporophylls, and are found scattered irregularly around the base of the plant.

Under normal conditions the seed does not undergo any resting condition and by April or May, some fifteen or sixteen months after fertilization, germination may occur. At such time the soft coloured outer coat of the testa has either dried to a thin irregular layer or has completely decayed, leaving the stony layer exposed. In the region of the micropyle radiating cracks appear (Text-figs. 84 and 85). These fissures are due in particular to pressure exerted by the expanding coleorhiza, but also to the increasing bulk of the embryo in general. Gradually that portion of the integumentary zone which encircles the micropyle is split up into widely separated wedge-shaped masses (Text-fig. 86) from the centre of which the greenish coleorhiza protrudes (Text-fig. 87), turns downwards, and penetrates the soil. Its elongation anchors the seedling to the soil by which time the tip of the primary root becomes apparent at the free end of the coleorhiza, its emergence being effected partly by force. The ruptured coleorhizal tip is split into wedge-shaped segments similar to those already encountered at the micropylar end of the testa (Text-fig. 88). The root grows quickly at the expense of the stored material within the endosperm, becoming fleshy and stout in outline, and wrinkled on the surface (Text-figs. 89 and 90). The appearance of secondary roots follows, but certain of these located on the upper contractile region of the primary root are highly modified and appear as dichotomously branched, coralloid masses (Text-figs. 91–93). These are apogeotropic in nature and usually occur in two groups on opposite sides of the tap-root, the surface of which has, meanwhile, become uneven and roughly patterned, owing in part to the formation of a protective periderm. The young sporophyte frees itself from the testa until all but the tips of the cotyledons



Text-figs. 84-93.—Series of drawings illustrating the germination of the seed and establishment of the seedling. Figure 85 represents a seed in longitudinal section and shows the hard outer coat of the testa, the membranous remains of the nucellus, a bulky endosperm enclosing an embryo in which the separate cotyledons and young root within the coleorhiza are depicted. For further details see text. The serrated nature of the pinnae is evident (figures 92 and 93); this character is absent from older plants. × 8/15.

are withdrawn (Text-fig. 90). The latter, acting as haustorial organs, draw on the food supply stored in the endosperm, until this is exhausted, when the empty shell of the testa and the withered cotyledons become detached. During this period also the curved outline of the first leaf, covered by protective hairs, appears between the exposed parts of the two cotyledons (Text-fig. 91).

Subsequently, the root system continues to develop, the tap root extending to a length of some fifteen inches, while at its thickest part a diameter of one and a half inches is attained (Text-fig. 93). At the same time, secondary and tertiary roots have multiplied, the coralloid mycorrhizal system being specially massive, much branched, and protruding above ground.

Such structures are an outstanding feature of a seedling during the first few years of its growth, but, although they persist, they are relatively inconspicuous in the

mature plant. In transverse section an "algal zone" is easily discernible to the naked eye, although the prominence of this area varies with the edaphic conditions, being specially well-formed in plants growing in rich, loamy soils, or under cultivation in gardens or glass houses. The appearance of the second leaf follows about a month after the first has unfolded; thereafter leaf production is exceedingly slow and only five or six leaves may arise in the first three years of growth.

A conspicuous feature of the pinnae of young plants is the serrations found near their tips (Text-figs. 92 and 93). These, however, are evanescent and gradually disappear with increasing maturity of the plants which, on reaching the age of ten to twelve years, are quite devoid of such vestiges. The presence of these features in young plants is regarded as evidence that the serrated margin was a permanent structure in the ancestral form of *Macrozamia spiralis*.

A survey of the facts disclosed by this investigation shows that certain peculiar features, namely, the archegonial neck-cells occasionally being in excess of two, and polyembryony due to sporophytic budding of the embryo, are common to *Macrozamia* and *Encephalartos* (Saxton, 1910). In addition, the average number of sporangia per sporophyll in *Macrozamia spiralis* is 342, and in *Macrozamia Miquelii* 503 (Chamberlain, 1935, p. 115). The mean of these numbers, 422, lies between those given for *Encephalartos caffer*, 567, and *Dioon edule*, 295, as supplied in Chamberlain's list. Again, in *Encephalartos* and *Macrozamia* (Coulter and Chamberlain, 1917) numerous vascular bundles are found in the pith, while all cones are lateral, and stem growth is monopodial.

The above features taken in conjunction point to the conclusion that *Macrozamia* has a closer affinity with *Encephalartos* than with any other cycadean genus.

Summary.

Macrozamia spiralis is distributed along some one thousand miles of the south-eastern coastal region of Australia. The body-form is modified by the prevailing edaphic conditions and the operation of contractile roots. Cones always arise laterally. Cones weighing as little as 0·6 gram were examined and by using certain specified precautions in the *modus operandi* these minute strobili may be detected and removed without destroying the plant.

The comparative rates of development in the component parts of the staminate and ovulate cones are presented in tabulated form.

The division of a deep-seated megaspore mother-cell results in the formation of three cells; the chalazal one persists as the functional megaspore.

The development of the female gametophyte is normal. Irregularly-shaped or malformed archegonial chambers occasionally occur.

The development of the microsporangium exhibits no unusual features.

The slit of dehiscence is defined by a band of thin-walled tissue, which is four cells in breadth. Pollination is anemophilous.

The growth of the male gametophyte is normal for cycads. Evidence is presented to show that the atmosphere of the archegonial chamber is saturated with moisture. Prior to fertilization the sperms swim actively in the pendent generative region of the male gametophyte, and are subsequently ejected into the archegonial chamber, whence they pass between the greatly dilated neck-cells into the egg. In some ovules the neck of the archegonium is comprised of four cells. An interval of two months intervenes between pollination and fertilization.

The method of entry by the sperms into the egg is discussed. Numerous male gametes may enter one egg. The behaviour of the male and female nuclei during fertilization is described. The division of the nucleus of the zygote was observed. Free simultaneous nuclear division follows: later, wall-formation is initiated.

At maturity the proembryo is cellular throughout, and remains so. Polyembryony arises from two causes: first, by the fertilization of more than one egg in a single female prothallus, and second, by sporophytic budding from the proembryo, almost any cells of which may become actively meristematic and give rise to an embryo. Only one embryo in a seed reaches maturity.

The seed germinates without any resting period, and produces a seedling having a contractile tap root, bearing abundant apogeotropic roots with prominent algal zone.

The results of this investigation substantiate the view that *Macrozamia* is more closely related to *Encephalartos* than to any other cycadean genus.

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EXPLANATION OF PLATES XIV-XVII.

Plate xiv.

1.—General view of a dense society of *Macrozamia spiralis* in open eucalyptus forest. 10 Jan., 1939. Narooma, N.S.W.

2.—Seed plant of *Macrozamia spiralis*. A few leaves have been excised in order to expose two cones, almost mature, and averaging ten and three quarter pounds in weight. The leaf bases and organic apex are buried in the soil. 10 Jan., 1939. Narooma, N.S.W.

3.—Microsporangiate plant of *Macrozamia spiralis* bearing ten mature cones, seven of which are visible. 10 Jan., 1939. Narooma, N.S.W.

4.—Single plant growing in a quartzite soil with trunk protruding some thirty inches above ground. 10 Jan., 1939. Dalmeny, N.S.W.

5.—Part of plant showing stem rising almost three feet above soil level, and enclosed in an armature of tough leaf bases. 10 Jan., 1939. Dalmeny, N.S.W.

6.—Apex of trunk partly cut away to show young leaves and position of organic apex. 10 Jan., 1939. Dalmeny, N.S.W.

Plate xv.

7.—Immature megasporangiate cone showing sporophylls, each with characteristic prolonged upturned process, and exposed ovules, which are marginal in position. 29 Dec., 1939.

8.—Mature megasporangiate (*a*) and microsporangiate (*b*) cones compared. The pollen has been shed from the latter. 27 Jan., 1939.

9.—Series of megasporophylls (*E-I*) and microsporophylls (*e-h*) showing relative sizes and shapes at intervals throughout development. *Dates of collection*: *E*, 14/4/38; *F*, 6/7/38; *G*, 4/11/38; *H*, 8/12/38; *I*, 22/2/39; *e*, 12/6/38; *f*, 4/10/38; *g*, 4/11/38; *h*, 20/12/38. × 0·42.

10.—Two microsporophylls from previous figure. *a*, just prior to dehiscence, and *b*, after dehiscence. In (*a*) the soral arrangement and line of dehiscence of the sporangia are clearly shown, while in (*b*) the sporangia gape widely and have shed their spores.

Plate xvi.

11.—Central apical region removed from a seed plant. The organic apex has produced, and is hidden amid numerous yellowish-white leaves, while laterally are situated three bud-like structures, each consisting of brown, furry, protective leaves encasing a strobilus. 3 Feb., 1940.

12.—Bud with some of the outer proximal leaves removed in order to expose the minute enclosed ovulate cone, which weighed 1·3 grams. The megaspore mother-cell was present in this material. 20 Jan., 1940.

13.—Microsporangiate cone, weight 11·0 grams. 3 Feb., 1940.

14.—Megasporangiate cone enclosed by the younger protective leaves. Feb. 8, 1940.

15.—Series of young megasporophylls (*A-D*) and young microsporophylls (*a-d*) showing comparative rates of development. *Dates of collection*: *A*, 20/1/38; *B*, 9/2/38; *C*, 11/3/38; *D*, 7/5/38; *a*, 20/1/38; *b*, 3/2/38; *c*, 11/3/38; *d*, 2/4/38.

16.—Photomicrograph of male nucleus almost enveloped by the nucleus of the egg. The finely granular nature of the former as compared with the coarsely granular appearance of the latter is evident. 10 March, 1939. × 117.

Plate xvii.

17.—Longitudinal section through female gametophyte showing deep archegonial chamber, and evidence of several proembryos with long coiled suspensors; the meristematic tips have burst through the egg membrane and are invading the endosperm. 10 March, 1939. × 7⅛.

18.—Section somewhat similar to that immediately preceding, but illustrating more clearly the lower part of a suspensor and an apical meristem. The clear region in the endosperm adjoining the egg membrane shows a notable absence of starch: this food reserve has been used to nourish the developing proembryos. 10 March, 1939. × 13⅛.

19.—High-power study of portion of above figure to show the elongated cells of the suspensor, and the apical meristem. 10 March, 1939. × 28.

20.—Apical meristem under still higher power of magnification. The invasion of the endosperm by the enzyme activity of the densely cytoplasmic cells of the meristem is clearly revealed. 10 March, 1939. × 133.

21.—Two active meristems growing side by side, and occupying the lowermost region of the proembryo. 10 March, 1939. × 200.

22.—Longitudinal section of part of female gametophyte showing parallel development of five embryos which have originated in different archegonia. The gradual disappearance of starch from the endosperm cells around these embryos is very apparent. 10 March, 1939. × 30.

TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XIX.

GENERA NOT PREVIOUSLY DISCUSSED.

By Consett Davis, M.Sc., Lecturer in Biology, New England University College.

(Twenty-three Text-figures.)

[Read 27th November, 1940.]

Twenty-six genera have been dealt with already in this series of papers. The purpose of the present paper is to summarize our knowledge of the remaining ten genera in the Order, less fully in the case of the two North American genera, as these two genera are being considered in detail by Mr. E. S. Ross, of the University of California, rendering repetition of the data unnecessary.

Genus Embonycha Navás 1917.

Insecta, *Revue illustrée d'Entomologie*, Rennes, Nos. 73–84, p. 15. Genotype, *Embonycha interrupta* Navás, 1917, l.c., fig. 11.

Asiatic Embioptera, the males winged, with R_{4+5} forked, M simple, cubitus with one anterior branch. First segment of left cercus one-segmented, strongly incurved, terminally subacute.

Embonycha interrupta Navás 1917, l.c. Fig. 1.

♂ (after Navás, l.c.). Length 11 mm., of forewing 9·5 mm., of hindwing 8·3 mm. General colour dark brown, head almost black, labrum ferruginous, last abdominal segment pale; wings with dark-brown bands, and with hyaline inter-venal lines and transverse striae at cross-veins. Terminalia (Fig. 1, after Navás, l.c., fig. 11) with left cercus one-segmented, curved inward and upward, apical third incrassate, especially exteriorly, apex tapered; right cercus with two long cylindrical segments. Whether the left cercus is echinulate is not stated.

♀ unknown.

Locality.—Indo-China: Chapa, 11/6/16, Vitalis de Salvaza (holotype ♂, Navás Collection).

This appears to be a very interesting insect, but the data concerning it are too meagre to draw any very definite conclusion. Its nearest relative seems to be *Ptilocerembia* Friedrichs (East Indies), in which the second segment of the left cercus is present as a small subconical protuberance on the outer side. The venation agrees with *Ptilocerembia*, differing therefore from *Burmitembia* and *Notoligotoma*, which have R_{4+5} simple (some forms of *Notoligotoma* are wingless). These four genera, with the wingless *Metoligotoma*, appear to form one unit (family); the distribution is compact (Burma, Indo-China, East Indies, Australia and Tasmania; Miocene–Recent). The series seems to be characterized by reduction or loss of the second segment of the left cercus (♂), by fusion with the first segment, followed in some cases by the loss of R_5, or of the entire wings. This is the opposite to the sequence leading by way of *Mesembia* to *Anisembia* (infra), in which R_5 is lost, and, subsequently, the left cercus reduced.

It is likely that *Embonycha* will prove to have two hind metatarsal bladders, the normal number for *Burmitembia*, *Notoligotoma* and *Metoligotoma* (the character is not detailed for *Ptilocerembia*; infra).

The details given by Navás (l.c.) for the tenth tergite of *Embonycha interrupta* may well be doubted, and probably derive from a cursory examination of the dried, unprepared terminalia. The left lobe of the tenth tergite is said to be undivided (? from

the right; cf. fig. 1), and produced backward as a blunt tubercle. As no suture is shown in the figure between the base of either of the cerci and the tenth tergite, the omission of a suture between the hemitergites, in figure and in verbal description, may well be classed as an oversight.

The type (if still extant) requires re-examination. The family classification and name are discussed in the next part of this series.

Genus Ptilocerembia Friederichs 1923.

Capita Zoologica, Deel ii, Afl. 1, p. 24. Genotype, *Ptilocerembia roepkei* Friederichs, 1923, l.c., figs. 5–7.

Embioptera occurring in the East Indies, the males with the following characters: Winged, R_{1+5} forked, M and Cu_{1a} simple; antennal segments with very long perpendicular hairs; tenth abdominal tergite completely cleft, with a trapezoidal sclerite basally separating the hemitergites; right hemitergite with an internal dorsal hook curved forward; process of left hemitergite simple; first segment of left cercus clavate, echinulate, second reduced, subconical, set firmly on outer part of distal end of first. Right cercus with two subcylindrical segments.

Ptilocerembia roepkei Friederichs 1923, l.c. Figs. 2–3.

♂ (after Friederichs, l.c., and 1934, p. 405 et seq.). Length 14–16 mm. (examples from culture under less favourable conditions 10½–12 mm.); length of (? fore-)wing 12–13 mm. General colour very dark brown, paler ventrally; wings brown with hyaline inter-venal lines. Head with large prominent subreniform eyes; sides behind eyes narrowed. Antennae with up to 30 segments, with long perpendicular hairs. Wings (Fig. 2, after Friederichs, 1923, fig. 6) with R_1, main stem of cubitus, and anal, distinct and strong, other veins weak, terminally subobsolescent, especially R_5, M and Cu_{1a}. R_1 confluent with R_{2+3} distally. Some four cross-veins from R_1 to R_{2+3}, one from M to radial sector. Details of hind tarsi not stated; metatarsal bladders probably two, by analogy with the closely-related *Notoligotoma*.

Terminalia (Fig. 3, after Friederichs, 1923, fig. 7) with tenth abdominal tergite completely cleft; hemitergites separated basally by a trapezoidal plate. Right hemitergite (10R) transverse, inner margin ending posteriorly in a subobtuse process ($10RP_1$), anteriorly in a dorsal hook curving forward ($10RP_2$). Left hemitergite (10L) with inner margin produced backward to an elongate process (10LP), medially slightly expanded, terminally subacute. Right cercus with two subcylindrical segments (RC_1, RC_2); first segment of left cercus (LC_1) clavate, dilated inward in an echinulate lobe in the terminal third; second segment (LC_2) shorter, subconical, firmly set on first segment outside and distad to inner dilation. Left cercus-basipodite curved outward, subacute.

♀ (after Friederichs, l.c., 1923 and 1934). Length 12–19 mm. General colour paler than in the male, mottled.

The recognition of the forma *dimidiata* Friederichs (1934, p. 406), representing a female of slightly different colour, not corresponding exactly to any geographic range, serves no useful purpose. Such colour-differences are frequently due to method of preservation, and to degree of melanization after the final ecdysis.

Locality.—Java (Smeroe and Soember Soeko Tangkep, near Malang; Bangelan, Kawi; Soember Asin) and Sumatra (Limau Manis). Location of types not stated.

This interesting genus is very closely related to the Australian genus *Notoligotoma*, in which, however, R_5 has been lost. The terminalia agree almost exactly; whether $10RP_2$ is echinulate in *Ptilocerembia* as it is in *Notoligotoma* is not stated. *Notoligotoma* has not the peculiar antennae of *Ptilocerembia*. The number of hind metatarsal bladders will probably prove to be two. Several years ago I made a cursory examination of a female of *Pt. roepkei* (determined by Friederichs; on loan from the Zoological Museum, Buitenzorg, Java; now in the Leyden Museum), but did not at the time realize the importance of the tarsal bladders; the number is not included in my notes.

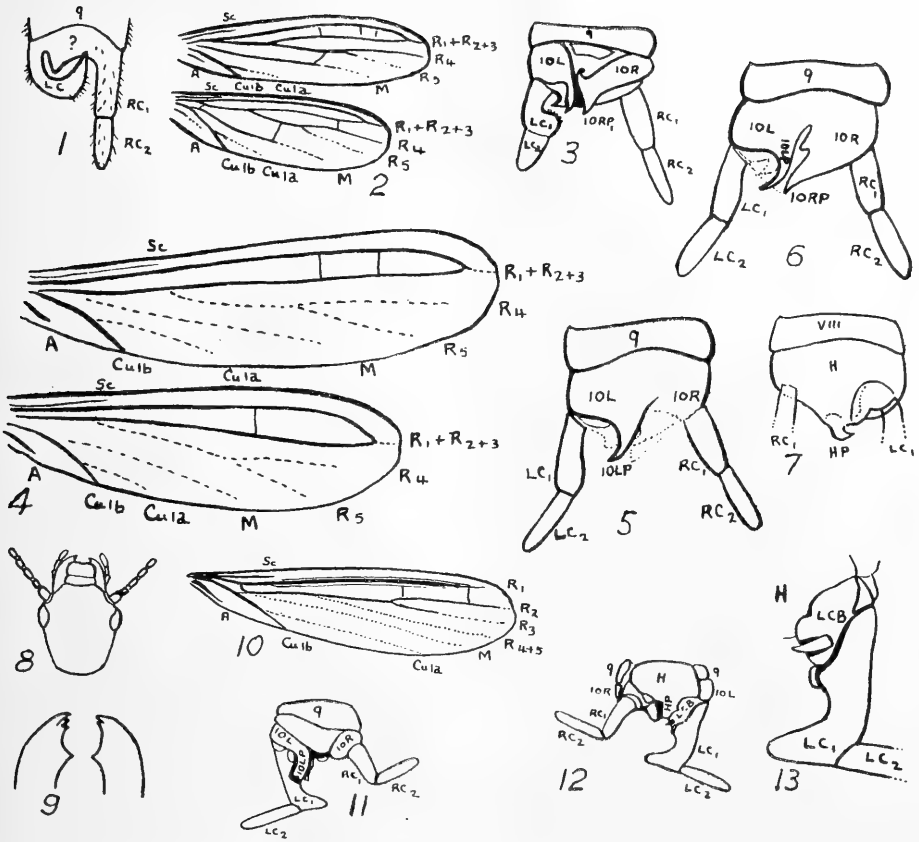

Fig. 1.—*Embonycha interrupta* Navás, holotype ♂. Terminalia from above. (After Navás, 1917, fig. 11; magnification not stated.)

Figs. 2-3.—*Ptilocerembia roepkei* Friederichs, ♂. 2. Right fore- and hindwing (diagrammatic). 3. Terminalia from above. (After Friederichs, 1923, figs. 6-7; magnifications not stated.)

Figs. 4-7.—*Diradius pusillus* Friederichs, holotype ♂. 4. Right fore- and hindwing. 5, 6. Terminalia from above, arrangement of component parts varying. 7. Terminalia from below. (After Friederichs, 1934, figs. 7*d*, 7*a-c* respectively; magnifications not stated.)

Figs. 8-13.—*Teratembia geniculata* Krauss, holotype ♂. 8. Head from above. 9. Mandibles from above. 10. Right forewing. 11. Terminalia from above. 12. Terminalia from below. 13. Base of left cercus from below. (After Krauss, 1911, Pl. i, figs. 3, 3A-B, 3D-F respectively; magnifications not stated.)

Genus Notoligotoma Davis 1936*a*.

Proc. Linn. Soc. N.S.W., lxi, p. 244. Genotype, *Oligotoma hardyi* Friederichs 1914, *Rec. W. Aust. Museum*, i, 3, p. 241.

The following species are recorded:

N. hardyi (Friederichs), 1914, l.c.; Davis, 1936*a*, l.c., p. 245, figs. 8, 15, 22, 29, 36; Davis, 1940, Proc. Linn. Soc. N.S.W., lxv, p. 158, fig. 4.

N. nitens Davis, 1936*a*, l.c., p. 246, figs. 9, 16, 23, 30, 37, 39–41.

These species have been described in conformity with the descriptions of the present series (Davis, l.c.), and the repetition of the data seems unnecessary. In the first descriptions (1936*a*, fig. 8, 9), the trapezoidal plate basally separating the hemitergites was omitted; this is present, as a weakly-sclerotized plate, in both species (cf. Davis, 1940, l.c.), apparently as in *Ptilocerembia*.

Genus Metoligotoma Davis 1936.

Proc. Linn. Soc. N.S.W., lxi, 248. Genotype, *Metoligotoma reducta* Davis, 1936*a*, l.c., p. 248.

The following species have been described in conformity with the descriptions of the present series, and are therefore merely listed:

M. reducta Davis, 1936*a*.—*M. reducta reducta* Davis, 1936*a*, Proc. Linn. Soc. N.S.W., lxi, p. 248.—*M. reducta* Davis, 1938, ibid., lxiii, p. 227, figs. 1–4.

M. ingens Davis 1936*a*.—*M. reducta ingens* Davis, 1936*a*, l.c., p. 250.—*M. ingens* Davis, 1938, l.c., p. 235, figs. 31–37.

M. illawarrae illawarrae Davis, 1938, l.c., p. 230, figs. 5–8.

M. illawarrae septentrionis Davis, 1938, l.c., p. 232, figs. 9–12.

M. illawarrae telocera Davis, 1938, l.c., p. 233, figs. 15–22.

M. collina collina Davis, 1938, l.c., p. 233, figs. 23–26.

M. collina exigua Davis, 1938, l.c., p. 235, figs. 27–30.

M. pentanesiana Davis, 1936*b*, ibid., lxi, p. 254, figs. 1–2, 4, 6; 1938, l.c., p. 237, figs. 38–41.

M. extorris Davis, 1936*b*, l.c., p. 256, figs. 3, 5, 7; 1938, l.c., p. 237, figs. 42–66.

M. intermedia Davis, 1938, l.c., p. 239, figs. 67–70.

M. anomala Davis, 1938, l.c., p. 241, figs. 71–74.

M. brevispina Davis, 1938, l.c., p. 241, figs. 75–79.

M. convergens Davis, 1938, l.c., p. 242, figs. 80–83.

M. bidens Davis, 1938, l.c., p. 243, figs. 84–87.

M. pugionifer Davis, 1938, l.c., p. 243, figs. 88–92.

M. minima Davis, 1938, l.c., p. 245, figs. 93-96.

M. begae Davis, 1938, l.c., p. 245, figs. 97–101.

M. tasmanica tasmanica Davis, 1938, l.c., p. 246, figs. 102–105.

M. tasmanica bassiana Davis, 1938, l.c., p. 248, figs. 106–108.

M. tasmanica biloba Davis, 1938, l.c., p. 249, figs. 112–115.

M. rileyi Davis, 1940, Proc. Linn. Soc. N.S.W., lxv, p. 155, figs. 1–3.

The genus extends along the east coast of Australia, from South Bruni Island, Tasmania, at least as far north as Townsville, Queensland. It is probably a direct descendant of *Burmitembia* Cockerell (Burmese Amber, ? Miocene), which differs in the presence of wings, and the lack of nodules on the left cercus, and possibly in the structure of the hemitergites (not known for *Burmitembia*). These two genera are also closely related to *Embonycha* Navás.

Genus Diradius Friederichs 1934.

Arch. f. Naturg., N.F., Bd. 3, Hft. 3, p. 419. Genotype, *Diradius pusillus* Friederichs, 1934, l.c., p. 419, figs. 7*a–d*.

Very small Neotropical Embioptera, the males with the following characters: Winged, R_{4+5} forked, M and Cu_{1a} simple; these veins are represented only by macrotrichia and bordering pigment-bands. Terminalia agreeing with *Oligembia* Davis (first segment of left cercus not echinulate; division of tenth abdominal tergite into hemitergites obsolete proximally) except in the process of the left hemitergite, which is simple, acutely tapered (complex, bifid, in *Oligembia*), and in the left cercus-basipodite, which seems to be weaker than in *Oligembia*.

Diradius pusillus Friederichs 1934, l.c. Figs. 4–7.

♂ (after Friederichs, l.c.). Length 4·5 mm.; length of forewing 3·6 mm., of hindwing approx. 2·5 mm. General colour mid-brown, antennae and palps brownish-yellow, wings brownish with broad hyaline inter-venal lines. Eyes moderately large, sides of head behind eyes rounded, converging posteriorly. Antennae incomplete; mandibles slender. Details of hind tarsus not given; possibly the same as in *Oligembia*, with no metatarsal bladder. Wings (Fig. 4, after Friederichs, l.c., fig. 7*d*) as in generic description, one or two cross-veins from R_1 to R_{2+3}. Terminalia (Figs. 5–7, after Friederichs, l.c., figs. 7*a–c*) with tenth abdominal tergite divided to left and right hemitergites (10L, 10R), division obsolescent proximally. Process of 10L (10LP) acutely tapered, curved to the left. Posterior process of 10R ($10RP_1$) subobtuse; inner margin of 10R notched. Left cercus with two subcylindrical segments (LC_1, LC_2), the first slightly dilated distally, but without nodules. Right cercus with two subcylindrical segments (RC_1, RC_2).

Hypandrium (H) with a terminal hook (HP), directed to the left. Structure of basipodites not stated, the left without the complex processes found in *Oligembia*, to judge from Figure 7.

♀ unknown.

Locality.—Isabelle, Humboldt region, State of Santa Cattarina, Brazil, coll. W. Ehrhardt. Holotype ♂ in Mus. Hamburg.

Genus Teratembia Krauss 1911.

Zoologica, Hft. 60, Bd. 23, p. 33. Genotype, *Teratembia geniculata* Krauss 1911, l.c., p. 33, Pl. i, figs. 3, 3A–G.

Very small Neotropical Embioptera, the males with the following characters: Winged, R_{2+3} forked, R_{4+5}, M, and Cu_{1a} simple; R_3, R_{4+5}, M, and Cu_{1a} subobsolescent. Tenth tergite with complex divisions and processes, homologies uncertain. First segment of left cercus not echinulate, incurved terminally to an obtusely-tapered lobe, and with a small medial internal protuberance; second segment of left cercus, and both segments of right cercus, subcylindrical. Structures at base of left cercus complex.

Teratembia geniculata Krauss 1911, l.c. Figs. 8–13.

♂ (after Krauss, l.c.). Length 5 mm., of forewing 4 mm. General colour brownish-yellow, head and pronotum brown, wings weakly banded with brown. Head (Fig. 8, after Krauss, l.c., Pl. i, fig. 3) with sides converging strongly behind eyes; antennae defective. Mandibles (Fig. 9, after Krauss, l.c., fig. 3A) each with an internal tooth half-way from base to apex, the left with three, the right with two terminal incurved teeth. Wings (Fig. 10, after Krauss, l.c., fig. 3B) as in generic description, R_1 not confluent with R_2. Terminalia (Figs. 11–13, after Krauss, l.c., figs. 3D–F) complex; tenth tergite with a medial plate, transverse, convex behind; on the right is a small sclerite, rounded, apparently without any process, placed at the base of the right cercus on the dorsal aspect; on the left, and posterior to the median plate, is another dorsal sclerite, with a process directed inward, curving backward and outward, weakly bifid terminally. This sclerite may be regarded as the left hemitergite (10L) and process (10LP), and the small sclerite, dorsally contiguous with the base of the right cercus, as the right hemitergite (10R); Krauss (l.c.) considers that they are the cercus-basipodites, and that the medial transverse plate is the undivided tenth tergite. The dorsal position of the lateral sclerites precludes this interpretation, as cercus-basipodites are ventral structures. Enderlein (1912, p. 99) considers the left-hand sclerite as a hemitergite, but labels the main transverse plate as the right hemitergite (l.c., fig. 63, rtg_{10}), and does not name the right-hand sclerite. The homology of the parts is by no means easy to establish from Krauss's description; he also refers to the right cercus-basipodite at one stage when the context clearly shows that he means the left cercus-basipodite (in his sense; 10L and 10LP of this paper). This error has been overlooked by Enderlein (l.c.) in his transcription of the data.

Below 10LP is a small process, terminally expanded, with jagged edges, and produced to the left in a blunt hook (figured in *ventral* view, Krauss, l.c., Pl. i, fig. 3G). The homology is uncertain; it may represent the more antero-dorsal part of a complex cercus-basipodite, or the remains of the left half of the larval tenth sternite. This region is also complex in *Oligembia* Davis (1939), which is probably related to *Teratembia*.

First segment of left cercus (LC_1) without nodules; LC_1 produced inward distally as an obtusely-tapered beak; inner margin, basad to this beak, with two obtuse medial protuberances, one above the other; second segment (LC_2) and segments of right cercus (RC_1, RC_2) subcylindrical. A pad-like ventral structure at the base of the left cercus probably represents the true left cercus-basipodite, or part of it; it carries a small acute peg directed inward. Hypandrium (H) produced backward in a tongue-like process (H.P.).

♀ unknown.

Locality.—Tucuman, Argentina, coll. Vezenyi, 15/1/1906 (holotype ♂, Mus. Buda-Pesth).

On the present data, there seems sound justification for Krauss's family (Teratembiidae), though based on a single genus, species, and specimen. However, further research may show that the venation of the type is teratological. This is the only case known in the whole Order in which R_{2+3} is forked. A possible explanation is that R_1 has become detached from the stem R_{1+5}, and secondarily attached to R_{2+3}. This would indicate a close affinity of *Teratembia* to *Oligembia* and *Diradius*. Breaking of the connection of a branch of R_{1+5} from the stem has been noted as an anomaly (confined to one wing) in *Oligembia* (Davis, 1939). *Teratembia* agrees with *Oligembia* and *Diradius* in the small size and subobsolescent venation, as well as in the geographical region inhabited. It agrees with both in the lack of nodules from the first segment of the left cercus, and with *Oligembia* in the complexity of the structures (whatever their homologies) at the base of the left cercus; this last character is not known for *Diradius*. *Teratembia* agrees with *Oligembia*, but differs from *Diradius*, in the complexity of the process of the left hemitergite (on the present interpretation). It appears to differ from both these genera in the complete division from the median plate of the two lateral sclerites here interpreted as hemitergites; in the apparent lack of any process from the right hemitergite in this sense; and in the form of the first segment of the left cercus (subcylindrical to weakly clavate in *Oligembia* and *Diradius*).

Krauss (l.c.) states that the hind legs of the unique type of *Teratembia geniculata* are missing; comparison of the tarsi with *Oligembia* is therefore impossible.

Genus Protembia Tillyard 1937.

Amer. J. Sci., xxxiii, p. 241. Genotype, *Protembia permiana* Tillyard 1937, l.c., figs. 1–2.

Permian Embioptera (Kansas beds), the females probably winged. Sc reaching to one-half the length of the wing, with a humeral veinlet. R three-branched, M two-branched. Cerci with more than two segments.

Protembia permiana Tillyard 1937, l.c. Fig. 14.

By the courtesy of the late Dr. R. J. Tillyard, I was enabled to examine the type in Sydney before it was returned to the Yale University Collection. The venation is substantially as in Figure 14. Dr. Tillyard believed that the type represented a female, a conical structure at the end of the abdomen being interpreted as the ovipositor. On the type specimen, this structure might as well represent the hypandrium, so that material proof that the females of *Protembia* were winged is, in my opinion, lacking; it is quite probable, however, that the loss of wings in the female had not occurred at that early date.

The head of the type appears to be broader than long, and the cerci composed of an unknown (probably large) number of annular segments, both characters in contrast to Tertiary and Recent Embioptera. The nature of the fore tarsi is not clear; it cannot be stated whether they were modified for spinning.

Locality.—Lower Permian of Kansas, U.S.A. I understand that Dr. F. M. Carpenter, of Harvard University, has obtained some more complete specimens of this genus, details of which will be published shortly.

Genus Tillyardembia Zalessky 1937.

Nature, 140, p. 847. Genotype, *Tillyardembia biarmica* Zalessky 1937, l.c.

This genus, from the Permian of Russia, is allowed as distinct only on the factors of locality and horizon; preservation of the specimens is not good enough to show any structural points.

Tillyardembia biarmica Zalessky 1937, l.c.

On the published data, little can be said of the structure of this species. It appears to be closely related to *Protembia permiana*, but is somewhat smaller. Zalessky also believed his specimen to be a winged female, but the means of determining the sex seem less apparent even than in *Protembia permiana*. The location of the type is not stated.

Genus Anisembia Krauss 1911.

Zoologica, Hft. 60, Bd. 23, p. 75. Genotype, *Embia texana* Melander, 1902, *Biol. Bull.*, iii, 1–2, p. 19.

North American (Sonoran) and Antillean Embioptera, the males wingless, or winged, with R_{4+5}, M, and Cu_{1a} simple. First segment of hind tarsi probably with only one ventral bladder throughout the genus. Male terminalia with left cercus one-segmented, due to the fusion of the two larval segments; second segment sometimes present as an unsutured bulge on the outer part of the end of the first segment, sometimes completely resorbed. Left cercus echinulate, sometimes only weakly so. Tenth abdominal tergite completely cleft; right hemitergite without any prominent process on the inner margin; process of left hemitergite simple to weakly bifid.

The taxonomy of this genus is being treated by Mr. E. S. Ross, of the University of California. The species described at the time of writing are:

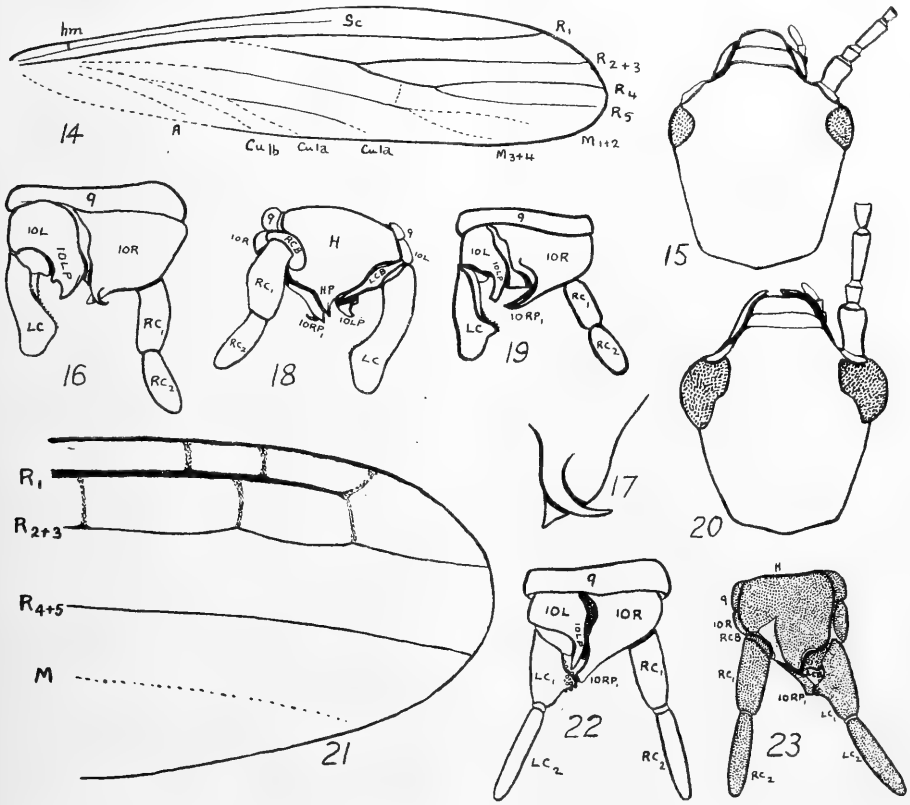

Fig. 14.—*Protembia permiana* Tillyard, type (? ♀). Right hindwing, × 9 approx. (From an unpublished figure by Tillyard, compared with the type by the writer.)

Figs. 15-18.—*Anisembia wheeleri* (Mel.), holotype ♂. 15. Head from above, × 30. 16. Terminalia from above, × 30. 17. Posterior part of right hemitergite from above, × 100. 18. Terminalia from below, × 30.

Fig. 19.—*Anisembia sini* Chamberlin, holotype ♂. Terminalia from above, × 17.

Figs. 20-23.—*Mesembia hospes* (Myers), paratype ♂. 20. Head from above, × 22. 21. Tip of right forewing, × 22. 22. Terminalia from above, × 22. 23. Terminalia from below, × 22, stippling in proportion to degree of sclerotization.

(Figs. 15-18, 20-23, based on camera lucida outlines; 19 prepared with constant use of an ocular micrometer. Conventional lettering for venation. Setae omitted. 9, Ninth abdominal tergite; 10L, 10R, left and right hemitergites of tenth abdominal segment; 10LP, process of 10L; $10RP_1$, posterior process of 10R; LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci; LCB, RCB, left and right cercus-basipodites; H, hypandrium; HP, process of H.)

Anisembia texana (Melander 1902).—*Embia texana* Melander 1902, l.c.—*Anisembia texana* (Mel.) Krauss 1911, l.c.—Austin, Texas (males winged or wingless). The type (♀) is in the Museum of Comparative Zoology, Harvard University. Melander (1903) has also described the male. The species is known also from Victoria, Texas.

Anisembia wheeleri (Melander 1902).—*Olyntha wheeleri* Melander 1902, l.c., p. 17.—*Anisembia wheeleri* (Mel.) Krauss 1911, l.c., p. 77. The unique type (♂) is wingless; collected at Cuernavaca, Mexico, it is now in the Museum of Comparative Zoology. The head and terminalia (drawn from the unprepared, alcoholic type) are shown in Figures 15–18.

Anisembia heymonsi (Enderlein 1912).—*Oligotoma heymonsi* Enderlein 1912, *Coll. zool. de Selys-Longchamps*, fasc. 3, p. 114, figs. 74–76.—*Anisembia heymonsi* (End.) Chamberlin 1923, *Proc. Calif. Acad. Sci.*, xii, 16.—Locality: Sierra Mixteca, Mexico; unique type ♂ in Mus. Berlin (winged).

Anisembia sini Chamberlin 1923, l.c.—The type ♂ (California Academy of Sciences, San Francisco) is from Lower California, Mexico (fig. 19). The only known males are wingless.

Note.—In addition to the above, three new species are being described by Mr. E. S. Ross, from Cuba, Mexico, and Arizona respectively, the last-named being at least subgenerically distinct.

Genus Mesembia Ross 1940.

(Printed paper not yet received).—Genotype *Oligotoma hospes* Myers, 1928, *Bull. Brooklyn Ent. Soc.*, xxiii, 2, p. 89.

Antillean Embioptera, the males winged, R_{1+5}, M and Cu_{1a} simple, hind metatarsus with only one ventral bladder. Male terminalia with tenth abdominal tergite completely cleft, right hemitergite without inner processes; first segment of left cercus clavate, echinulate, second segment distinct, subcylindrical, at least three times as long as thick.

I have not yet seen Mr. Ross's paper in print; I have read his manuscript, and have his assurance that his paper will appear well in advance of the present paper.

Mesembia hospes (Myers 1928).—*Oligotoma hospes* Myers 1928, l.c. The type series, from Soledad, Santa Clara, Cuba (Museum of Comparative Zoology), includes two males (holotype and paratype). The paratype is here figured (Figs. 20–23); the holotype has the terminalia badly distorted, due to the method of preparation, so that the figure given by Myers (l.c.) is misleading.

In addition to this species, Mr. Ross is describing a new species from Haiti, West Indies.

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TAXONOMIC NOTES ON THE ORDER EMBIOPTERA. XX.

THE DISTRIBUTION AND COMPARATIVE MORPHOLOGY OF THE ORDER EMBIOPTERA.

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(Four Text-figures.)

[Read 27th November, 1940.]

In the preceding nineteen parts of the present series, the available knowledge of the various genera of the Order Embioptera has been summarized, and certain new data added. In all, thirty-six genera have been allowed or described as new, while five (*Antipaluria*, *Dityle*, *Euembia*, *Aposthonia* and *Monotylota*) have been listed as untenable. Systematic order has not been followed in the treatment of genera, for several reasons. It has been desirable from the point of view of publication to treat the Order in a number of short papers rather than in one or a few large ones, so that the sequence followed is in part dependent on the avoidance of nomina nuda in cross-references. Moreover, the earlier parts were compiled at a time when it appeared that circumstances might preclude completion of the work, so that, where possible, the readily-available data were put on record regardless of sequence. It is the purpose of the present paper to arrange the genera in systematic order, with suggestions as to family classification, and to note certain points in the distribution of the Order, and evolutionary trends in the comparative morphology of its members.

Much of the work in the preceding papers of this series was of necessity carried out under hurried conditions. The types, and certain other material, of the Museum of Comparative Zoology, the British Museum, the Paris Museum, and the Oxford University, Genoa, Geneva and Congo Museums, were examined in a working time of three weeks, and the study of the unworked material from the first three of the above Museums, and the Colombo Museum, was carried out during several months, interspersed with academic duties and the compilation of the papers of this series for publication. These facts are offered both as an extenuation of the inadequacy which is apparent in certain parts of the series, and as a suggestion to future workers on the Order that a considerable amount of work still remains to be done even on the collections listed above, both in the study of points untouched by the writer and in checking the facts adduced.

Generic Key.

The following key, based on the characters of the mature males, serves to distinguish between the known genera. Structures referred to in the key are figured at some place in the earlier parts of the present series. The greatest difficulty lies in the separation of the genera *Rhagadochir* and *Pararhagadochir*, especially in the aberrant species *P. argentina* Navás (two hind metatarsal bladders), and in the supposedly East African species *Rh. carpenteri* Davis, which has terminalia generically inseparable from *Pararhagadochir*. This question has been discussed earlier (Part xv of this series). Another difficulty arises in that *Calamoclostes* End. may be based on a venational aberration.

The interpolation of several genera in the key between *Embia* Latr. and the very closely related *Parembia* Davis (separated only on the hind metatarsal bladders and on the distribution) illustrates the extremely arbitrary nature of the key. Again, the key might be rendered unworkable by the discovery of wingless forms of the male in genera now known only from winged males, e.g. *Mesembia*. The key is drawn up merely on the available data, and may require considerable modification in the light of future

records. In several cases, for convenience, a dichotomy has been formed on a character of relatively little importance, such as would not be allowed as a generic character unless supported by additional characters. Such supplementary characters, though omitted in the key, are of course included under the generic diagnoses in the earlier parts of the series.

1. Permian; cerci composed of numerous annular segments. (♀ probably winged) 2
   Tertiary-Recent; cerci with two segments or less. (♀ wingless) 3
2. North American ..... *Protembia* Tillyard
   Russian ..... *Tillyardembia* Zalessky
3. Left cercus two-segmented, not echinulate 4
   Left cercus echinulate (rarely smooth; if so, then the two segments fused to a composite structure) 10
4. Tenth abdominal tergite entire, or, if divided, processes of hemitergites small, not prominent; ventral parts of terminalia almost symmetrical ..... *Clothoda* Enderlein (syn. *Antipaluria* Enderlein)
   Tenth abdominal tergite wholly or partly cleft, processes of hemitergites large, prominent, often complex; ventral parts of terminalia markedly asymmetrical 5
5. R_{4+5} (or macrotrichia representing vein) forked 6
   R_{4+5} simple, or wingless 7
6. Process of left hemitergite simple ..... *Diradius* Friederichs
   Process of left hemitergite complex ..... *Oligembia* Davis
7. R_{2+3} forked ..... *Teratembia* Krauss
   R_{2+3} simple, or wingless 8
8. Right hemitergite with an inner ventral flap-like process 9
   Right hemitergite without any process on the inner side ..... *Saussurembia* Davis
9. Hind metatarsus with two prominent ventral bladders ..... *Haploembia* Verhoeff (syn. *Dityle* Friederichs)
   Hind metatarsus not as above ..... *Oligotoma* Westwood (syn. *Aposthonia* Krauss)
10. Second segment of left cercus reduced, wholly or partly fused to first segment 11
    Second segment of left cercus distinct, subcylindrical, at least three times as long as thick 16
11. R_{4+5} forked 12
    R_{4+5} simple, or wingless 13
12. Second segment of left cercus represented by a small obtuse protuberance on outer side of end of first segment ..... *Ptiloceremba* Friederichs
    Second segment of left cercus represented as a subacute incurved extension of first segment ..... *Embonycha* Navás
13. Right hemitergite with an internal echinulate process directed forward .. *Notoligotoma* Davis
    Right hemitergite not as above 14
14. Left cercus smooth; veins strong, with some oblique cross-veins; Miocene ..... *Burmitembia* Cockerell
    Left cercus echinulate (rarely almost smooth); veins weaker, with cross-veins weak, or wingless; Recent 15
15. Right hemitergite with a dorsal flap-like process directed inward; Australian ..... *Metoligotoma* Davis
    Right hemitergite not as above; American ..... *Anisembia* Krauss
16. R_{4+5} simple in all wings ..... *Mesembia* Ross
    R_{4+5} forked, at least in hindwings, or wingless 17
17. Left hemitergite with a short rounded dorsal protuberance on the right, but with main process simple ..... *Pseudembia* Davis
    Left hemitergite and process not as above 18
18. Process of left hemitergite simple, without an additional lateral or dorsal lobe 19
    Process of left hemitergite with an additional lateral or dorsal lobe 26
19. First segment of left cercus with an internal echinulate hook directed forward, longer than thick ..... *Leptembia* Krauss
    First segment of left cercus not as above 20
20. Hind metatarsus with two ventral bladders 21
    Hind metatarsus with one ventral bladder ..... *Embia* Latreille (syn. *Euembia* Verhoeff and *Monotylota* Enderlein)
21. Right hemitergite without any process on inner side; wingless ..... *Dictyoploca* Krauss
    Right hemitergite with an inner process; winged 22
22. Cubitus with three or more branches ..... *Berlandembia* Davis
    Cubitus two-branched 23
23. First segment of left cercus with inner margin carrying a row of large sharp forwardly-directed teeth, practically uniseriate ..... *Dinembia* Davis
    First segment of left cercus not as above 24

24. First segment of left cercus with inner margin produced into two lobes armed with strong teeth ..... *Metembia* Davis
First segment of left cercus with only one internal lobe, with rather small teeth 25
25. Inner process of right hemitergite flap-like, elliptical; medial hind metatarsal bladder large, rounded ..... *Parembia* Davis
Inner process of right hemitergite not as above; medial hind metatarsal bladder small, conical ..... *Embolyntha* Davis
26. R_{4+5} simple in forewing, shortly forked in hindwing ..... *Calamoclostes* Enderlein
R_{4+5} forked in all wings, the fork at least as long as the stem 27
27. Mandibles huge, overlying labrum ..... *Enveja* Navás
Mandibles not as above 28
28. Teeth on first segment of left cercus less than ten, very large 29
Teeth on first segment of left cercus small, more than ten in number 30
29. Hind metatarsus with one ventral bladder; M tending to fork ..... *Donaconethis* Enderlein
Hind metatarsus with two ventral bladders; M simple ..... *Odontembia* Davis
30. First segment of left cercus with more than one internal echinulate lobe; cubitus three-branched ..... *Dihybocercus* Enderlein
First segment of left cercus with one internal echinulate lobe; cubitus two-branched .. 31
31. R_{4+5} obsolescent beyond fork ..... *Navásiella* Davis
R_{4+5} not as above 32
32. Process of left hemitergite with a distal concavity between lobes 33
Process of left hemitergite with lateral lobe very short, no distal concavity between it and main part of process ..... *Parachirembia* Davis
33. Inner process of right hemitergite a flat subelliptical flap separated from hemitergite by membrane except at posterior limit 34
Inner process of right hemitergite not as above 35
34. Hind metatarsus with two large ventral bladders; right cercus-basipodite very large .... *Macrembia* Davis
Hind metatarsus with only one ventral bladder; right cercus-basipodite small .... *Chirembia* Davis
35. Hind metatarsus with two ventral bladders; African ..... *Rhagadochir* Enderlein
Hind metatarsus with one ventral bladder (two in one species); Neotropical .... *Pararhagadochir* Davis

Family Classification.

The following major groupings are advanced:

Sub-Order Protembioptera (Protembiaria of Tillyard 1937).

Family Protembiidae Tillyard 1937: *Protembia* Till., *Tillyardembia* Zal.

Sub-Order Euembioptera (Euembiaria of Tillyard 1937).

Family Clothodidae Tillyard 1937: *Clothoda* End.

Family Oligembiidae, n. fam.: *Oligembia* Davis, *Diradius* Fried.

Family Teratembiidae Krauss 1911: *Teratembia* Krauss.

Family Oligotomidae Krauss 1911: *Oligotoma* Westw., *Haploembia* Verhoeff.

Family Notoligotomidae, n. fam.: *Notoligotoma* Davis, *Metoligotoma* Davis, *Burmitembia* Ckll., *Embonycha* Nav., *Ptilocerembia* Fried.

Family Anisembiidae, n. fam.: *Anisembia* Krauss, *Mesembia* Ross, *Saussurembia* Davis.

Family Embiidae auct.: Remaining 20 genera.

In several cases (Oligembiidae, Notoligotomidae) prior genera (*Diradius, Embonycha, Burmitembia, Ptilocerembia*) have been passed over in the selection of the family stem, merely because existing descriptions of those genera do not allow their structure and relationship to be fully gauged.

The characteristics of the families are summarized below. Convergence prohibits the drawing up of a satisfactory family key based on structure alone, but in all except one genus the family sequence has been kept in the generic key. In the case of *Saussurembia*, which differs from *Mesembia* only in the lack of nodules on the left cercus, the desired sequence cannot be accomplished in the generic key.

(1) *Protembiidae*: Permian Embioptera, obviously very generalized in structure; the state of preservation of the fossils does not allow any very definite conclusions to be drawn. The venation is not much less reduced than in some recent Embioptera; the cerci were apparently multi-articulate. These fossils may form a link with the Protoperlaria. It seems probable that the female was winged.

(2) *Clothodidae*: The most generalized of recent Embioptera, Neotropical in range; the series *Clothoda nobilis* (Gerst.) → *C. intermedia* Davis → *C. urichi* (Sauss.) illustrates the division of the tenth tergite followed by the loss of the third cubital branch, the cerci remaining unchanged. The ventral structures of the male terminalia emphasize the primitive nature of the family, and its far removal from other recent forms. The Miocene *C. florissantensis* (Ckll.) has been provisionally referred to the genus *Clothoda*. The number of hind metatarsal bladders in this species is unknown; in the recent species, two bladders are present. This appears to be primitive, the medial bladder possibly representing the former point of articulation of two segments now fused.

(3) *Oligembiidae*: A Neotropical series including *Oligembia* and *Diradius*. The venation is greatly reduced in strength, although reduction in the number of veins is less marked than in some other genera, the traces of R_4 and R_5 remaining distinct. No hind metatarsal bladders seem to be present, but whether this is primitive is very doubtful. The terminalia agree with the Oligotomidae in the incomplete fission of the tenth abdominal tergite and the lack of nodules on the left cercus in the adult male. The structures at the base of the left cercus are complex in *Oligembia*, as they are in *Oligotoma*; details for *Diradius* are lacking. *Oligembia* appears to be derived from *Diradius* by the forking of the process of the left hemitergite, a frequently-recurrent evolutionary step in the Order. The family is probably not very close to the Oligotomidae, in spite of superficial resemblance. The general weakness of the veins in both families may be associated with small size.

(4) *Teratembiidae*: This Neotropical family is based on a single specimen, so that generalizations on the structure are unsafe. It appears to have R_{2+3} forked and R_{4+5} simple. If this is a constant feature, it indicates family distinction from the Oligembiidae. If, however, it represents an individual aberration (R_4 detached from R_{4+5} and secondarily attached to R_{2+3}), the Teratembiidae should be enlarged to include the Oligembiinae as a sub-family.

The structure of the terminalia has been discussed earlier (Part xix of this series). They agree with *Oligembia* in the lack of nodules on the left cercus, and the complex structures at the base of this cercus; in other respects they seem to differ markedly, but the exact structure and homologies are doubtful.

(5) *Oligotomidae*: The genus *Oligotoma* has as its indigenous range the warmer parts of the Asiatic region, extending throughout Australia, and possibly to East Africa. It is now tropicopolitan, due apparently to human transport. The recent species of *Haploembia* are distributed around the coasts of the Mediterranean and Black Seas.

Haploembia may temporarily be assigned to the Oligotomidae, a course suggested by Krauss. The family characters may be summarized as follows: Winged or wingless; if winged, veins weakly developed, R_{4+5}, M, and Cu_{1a} simple. Hind metatarsus with one or two ventral bladders. Male terminalia with tenth abdominal tergite incompletely separated into hemitergites; right hemitergite with an elongate posterior process and a ventral flap-like inner process; first segment of left cercus without nodules, second segment distinct, elongate-subcylindrical. Structures at base of left cercus often complex.

Some members of the next two families agree with the winged examples of *Oligotoma* in the absence of R_5, which cannot therefore be taken as a family character, as it has been in the past.

(6) *Notoligotomidae*: This name is selected for an apparently monophyletic series of Indo-Malayan and Australian distribution (Miocene to Recent), the common character of which is the partial or total fusion of the segments of the left cercus. The composite structure is usually echinulate (not in *Burmitembia*; only very weakly in *Metoligotoma rileyi* Davis). In some cases, R_5 is lost (*Burmitembia*, *Notoligotoma* pars), or winglessness supervenes (*Notoligotoma* pars, *Metoligotoma*). The processes of the hemitergites of the male terminalia are variable, but show no affinity to the Oligotomidae. Two hind metatarsal bladders probably characterize all members. The close relationship between *Ptilocercembia* and *Notoligotoma* indicates the impossibility of using the lack of R_5, unsupported by other factors, as the basis for a major dichotomy.

(7) *Anisembiidae*: This family culminates in the Sonoran genus *Anisembia*; forms linking this genus to more generalized types are probably the Antillean and Central American genera *Mesembia* and *Saussurembia*. These three genera are characterized by the loss of R_5 or of the entire wings, convergent to the two preceding families. *Anisembia* is further specialized by the fusion of the segments of the left cercus in the adult male. It is closely convergent to the two endemic Australian genera, but its ancestor (cf. *Mesembia*) would appear to have had R_{4+5} simple and the second segment of the left cercus distinct, whereas the ancestor of the Australian genera (cf. *Ptiloceremba*) would seem to have had R_{4+5} forked and the second segment of the left cercus fused to the first segment.

The processes of the hemitergites of the male terminalia are variable in the Anisembiidae, but the right hemitergite is always very clearly separated from the left, and lacks any marked trace of an inner process. One hind metatarsal bladder is probably the characteristic of the family as at present constituted. Nodules are present on the first segment of the ♂ left cercus in *Mesembia* and in *Anisembia* (sometimes weakly so), but absent in *Saussurembia*, possibly a secondary loss.

(8) *Embiidae*: This is very probably a polyphyletic group, but subdivision on the present data seems impossible. On this understanding, it may be retained as an artificial unit for members of the Order in which the venation and terminalia have reached a common stage in evolution. If wings are present, R_{4+5} is forked; in some cases M is normally or exceptionally forked, in others the cubitus has more than the usual two branches. The hind tarsi have one or two bladders on the first segment. In the male terminalia, the tenth tergite is always completely separated into hemitergites; the left hemitergite varies very considerably, but the right has a process on the inner margin except in *Dictyoploca*. The left cercus is two-segmented, the first segment being echinulate in all cases, the second elongate, subcylindrical and distinct.

The genera comprising the family occur in South America (one species reaching Central America) and Africa, extending thence east to East India and north to the southern parts of Europe. In spite of apparent structural homogeneity, the Embiidae may well be an unnatural group, e.g. *Embolyntha* may well be a link between the Clothodidae and the Anisembiidae, and more closely related in its ancestry to these families than to Old-World Embiidae. To follow this course would possibly seem to be giving prominence to zoogeography at the expense or exclusion of morphology.

The above eight families may be artificially keyed as follows; the key can be used only by considering locality* as well as structure:

1. Permian ..... Protembiidae
   Tertiary-Recent 2
2. Tenth abdominal tergite entire in the male or, if divided, processes of hemitergites small, not prominent; ventral parts of terminalia almost symmetrical ..... Clothodidae
   Male terminalia with processes of hemitergites prominent, often complex; ventral parts markedly asymmetrical 3
3. Indo-Malayan and Australian; left cercus one-segmented in the male .... Notoligotomidae
   Not as above 4
4. Central and North American and Antillean, R_{4+5} simple, or wingless ..... Anisembiidae
   Not as above 5
5. Male terminalia with hemitergites clearly separated ..... Embiidae
   Male terminalia with suture between hemitergites obsolescent basally, or if complete, hemitergites in contact 6
6. R_{2+3} apparently forked (♂) ..... Teratembiidae
   R_{2+3} simple or wingless (♂) 7
7. R_{4+5} or its trace forked (♂) ..... Oligembiidae
   R_{4+5} simple or wingless (♂) ..... Oligotomidae

Note.—Navás (1918) divided the Order into two Sub-Orders, Oryttica and Netica, one for the genus *Cylindracheta*, the other for the remaining genera. This seems quite unnecessary, as *Cylindracheta* is a Gryllotalpid.

Comparative Morphology and Evolutionary Trends.

In Figures 1–4, an attempt has been made to illustrate schematically the comparative morphology of those characters used in the Order as taxonomic criteria. The fact that

* The locality in which the group is indigenous, not the range enlarged by artificial spreading.

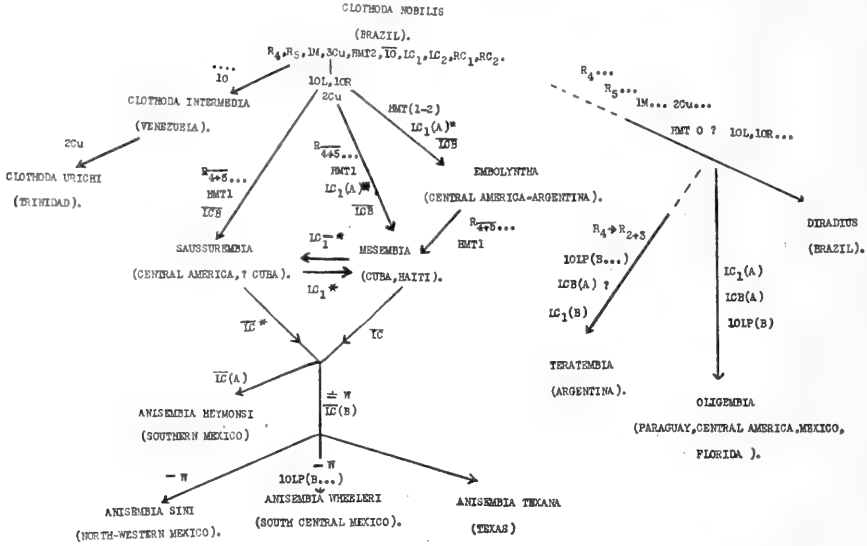

Fig. 1.

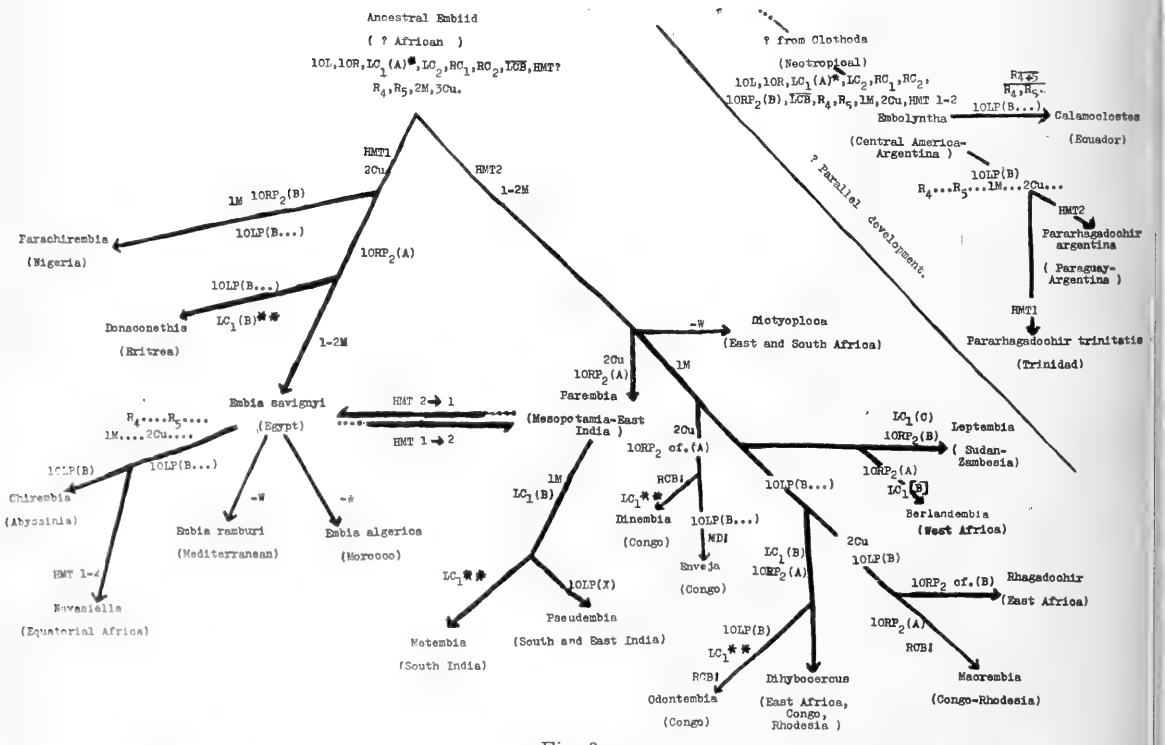

Fig. 2.

Figs. 1-4.—Comparative anatomy and possible evolutionary trends in the Order Embioptera. (1) New-World groups exclusive of the more advanced Embiidae. (2) Embiidae. (3) Oligotomidae. (4) Notoligotomidae. For codification of characters see text.

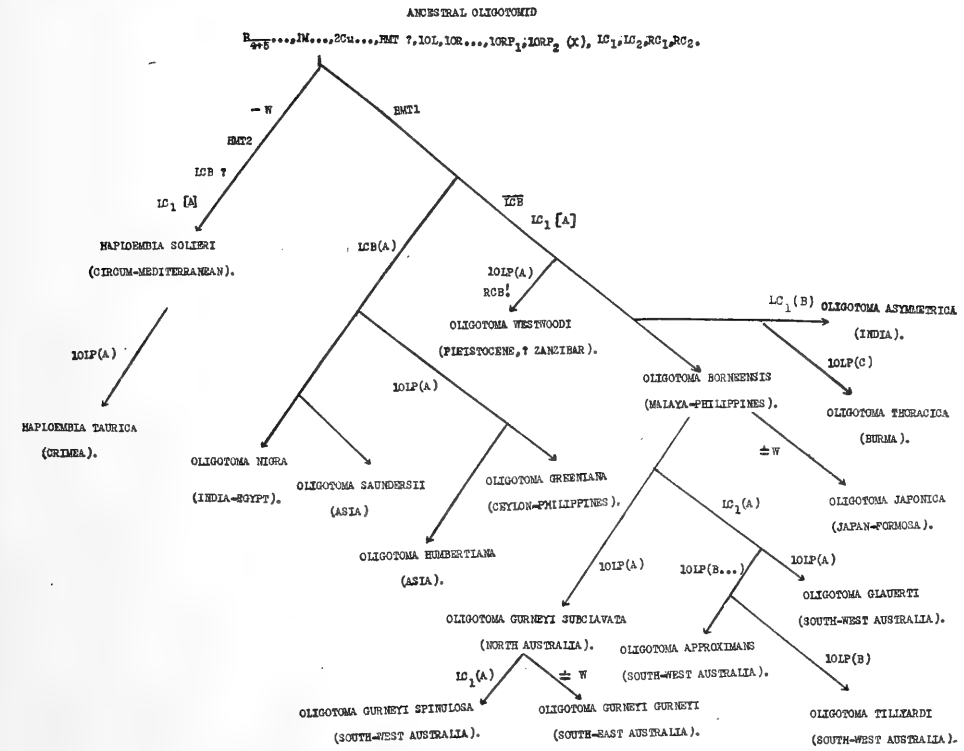
ANCESTRAL OLIGOTOMID
$R_{\overline{4+5}}$...,1M...,2Cu...,HMT ?,1OL,1OR...,1ORP$_1$,1ORP$_2$ (X), LC$_1$,LC$_2$,RC$_1$,RC$_2$.
− W
HMT2
LCB ?
LC$_1$ [A]
HMT1
$\overline{LCB}$
LC$_1$ [A]
HAPLOEMBIA SOLIERI
(CIRCUM-MEDITERRANEAN).
LCB(A)
1OLP(A)
RCB
OLIGOTOMA WESTWOODI
(PLEISTOCENE,? ZANZIBAR).
LC$_1$(B)
OLIGOTOMA ASYMMETRICA
(INDIA).
1OLP(C)
OLIGOTOMA THORACICA
(BURMA).
1OLP(A)
HAPLOEMBIA TAURICA
(CRIMEA).
1OLP(A)
OLIGOTOMA NIGRA
(INDIA-EGYPT).
OLIGOTOMA SAUNDERSII
(ASIA)
OLIGOTOMA GREENIANA
(CEYLON-PHILIPPINES).
OLIGOTOMA BORNEENSIS
(MALAYA-PHILIPPINES).
± W
OLIGOTOMA JAPONICA
(JAPAN-FORMOSA).
OLIGOTOMA HUMBERTIANA
(ASIA).
LC$_1$(A)
1OLP(A)
1OLP(B...)
1OLP(A)
OLIGOTOMA GLAUERTI
(SOUTH-WEST AUSTRALIA).
OLIGOTOMA GURNEYI SUBCLAVATA
(NORTH AUSTRALIA).
OLIGOTOMA APPROXIMANS
(SOUTH-WEST AUSTRALIA).
1OLP(B)
LC$_1$(A)
± W
OLIGOTOMA GURNEYI SPINULOSA
(SOUTH-WEST AUSTRALIA).
OLIGOTOMA GURNEYI GURNEYI
(SOUTH-EAST AUSTRALIA).
OLIGOTOMA TILLYARDI
(SOUTH-WEST AUSTRALIA).

Fig. 3.

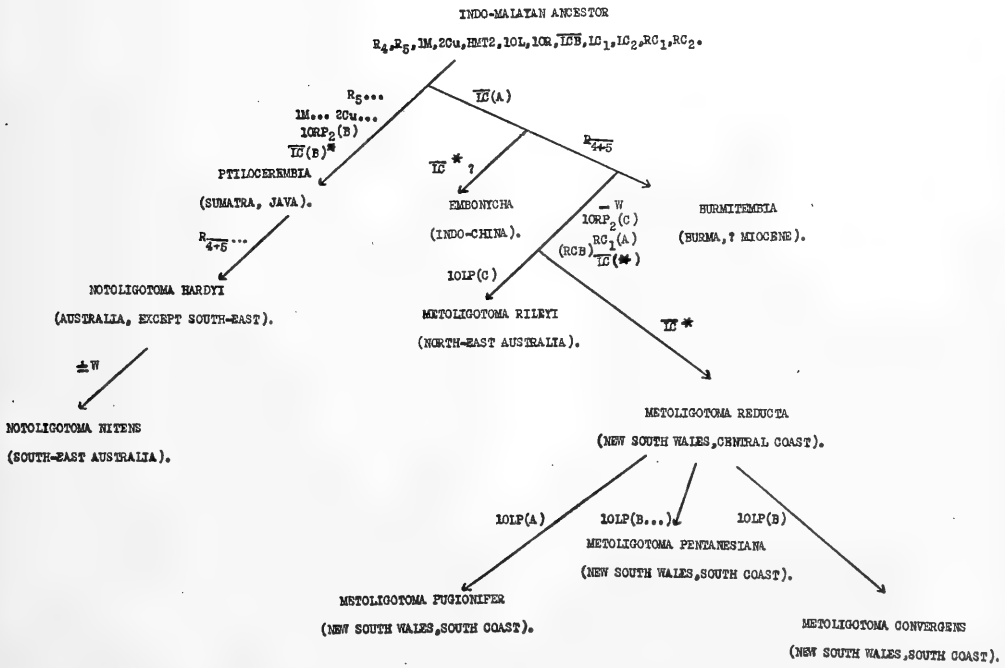
INDO-MALAYAN ANCESTOR
R_4,R_5,1M,2Cu,HMT2,1OL,1OR,$\overline{LCB}$,LC$_1$,LC$_2$,RC$_1$,RC$_2$.
R_5...
1M... 2Cu...
1ORP$_2$(B)
$\overline{LC}$(B)*
$\overline{LC}$(A)
$R_{\overline{4+5}}$
$\overline{LC}$ * ?
PTILOCEREMBIA
(SUMATRA, JAVA).
EMBONYCHA
(INDO-CHINA).
BURMITEMBIA
(BURMA,? MIOCENE).
$R_{\overline{4+5}}$...
NOTOLIGOTOMA HARDYI
(AUSTRALIA, EXCEPT SOUTH-EAST).
− W
1ORP$_2$(C)
RC$_1$(A)
(RCB) $\overline{LC}$(*)
1OLP(C)
METOLIGOTOMA RILEYI
(NORTH-EAST AUSTRALIA).
$\overline{LC}$ *
± W
NOTOLIGOTOMA NITENS
(SOUTH-EAST AUSTRALIA).
METOLIGOTOMA REDUCTA
(NEW SOUTH WALES, CENTRAL COAST).
1OLP(A)
1OLP(B...)
1OLP(B)
METOLIGOTOMA PENTANESIANA
(NEW SOUTH WALES, SOUTH COAST).
METOLIGOTOMA PUGIONIFER
(NEW SOUTH WALES, SOUTH COAST).
METOLIGOTOMA CONVERGENS
(NEW SOUTH WALES, SOUTH COAST).

Fig. 4.

these characters are selected by systematists is sufficient indication that little profit can accrue from a comparative study of most other characters; the internal anatomy is almost constant throughout the widely-separated members of the Order which have been studied. Possible supplementary characters for comparative purposes are to be found in the thoracic and anterior abdominal sternites, and in the female terminalia; these characters show little indication of differences useful for comparative purposes, at least at this stage of our knowledge; they may be found useful when further studies on the Order are carried out.

The scheme previously advanced (Davis, 1938, fig. 120) is obviously unsound in many places, particularly in the treatment of the 'Oligotomidae' and in the consideration of *Haploembia* and '*Monotylota*'. This scheme was prepared with very little first-hand knowledge of exotic genera. It was advanced to illustrate a theory of convergence, rather than as an attempt to solve the evolutionary problems in different lines of descent in the Order.

In the present schemes, and in the discussion below, the males alone are referred to. The schemes (Figs. 1–4) are primarily to show the comparative morphology of existing types; they may also indicate evolutionary relationships. In several cases, recent species are placed in the ancestral line of other recent species; this course has been explained previously (1938, fig. 120).

Two assumptions open to a considerable amount of doubt must be made if the schemes are taken as evolutionary, and not merely as comparative. The New- and Old-World Embiidae are shown as parallel developments, rather than as a unit; and the Old-World Embiidae are divided by the primary dichotomy on one or two hind metatarsal bladders. The second of these two steps is even less defensible than the first. It cannot be said whether one or two bladders represent the primitive condition; perhaps it is significant that all Tertiary fossils in which the character is preserved have two such bladders. In any case, a reversion to the primitive type (whatever it is), in such a simple character, may well have occurred in several instances. This would be in opposition to the so-called Dollo's Law, which is in any case not accepted. The artificiality of the dichotomy is illustrated in Figure 2 thus (*Embia* ⇆ *Parembia*).

Notes on Figures 1–4.

1.—This scheme shows the comparatively straightforward development within the Clothodidae; several possible courses for the development of the Anisembiidae; and an attempt to relate the difficult groups Teratembiidae and Oligembiidae to a more primitive form. The last-named is too hypothetical to discuss further. The course most favoured for the development of *Anisembia* is *Clothoda–Embolyntha–Mesembia–Anisembia*, with *Saussurembia* derived from *Mesembia* by a secondary degeneration of the nodules of the left cercus (by neoteny, since the larval cerci are smooth throughout).

2.—This tentative scheme would make the Embiidae polyphyletic. Convergence is frequently invoked, especially in the forking of the process of the left hemitergite, the loss of wings, and to a less extent the modification in several ways of the first segment of the left cercus.

3.—Assuming the Oligotomidae as at present constituted to be monophyletic, the comparison of its various component lines offers little difficulty, but the origin of the family as a whole from any other known type is shrouded in obscurity. Loss of wings, and development of a terminal hook on the process of the left hemitergite, are the most frequently-recurring parallel steps.

4.—The evolution of the Notoligotomidae offers less difficulty than that of other families. The ancestor might well resemble the Indian genus *Parembia*; on Figure 4, it has been assumed that the left cercus was not echinulate, but this difference from *Parembia* can be resolved by considering the loss of nodules on the left cercus as a secondary feature of *Burmitembia* and *Metoligotoma rileyi*, as suggested under *Saussurembia*.

The fusion of the segments of the left cercus is convergent to the genus *Anisembia*; an exactly parallel step (in both cerci) has occurred within the Nemouridae, in the closely-related Order Perlaria. The motive force in each case may well have been

surface tension acting on the cercus during the last ecdysis. This is not an implication of somatic induction; the growth mechanics of the left cercus, as of other parts of the complex terminalia, during the last ecdysis, must be complicated, and may include such factors as pressure of body fluid, muscular contraction, differential hardening, differential adherence to the exuvium, etc.; as soon as these forces were relaxed, by a genetic change, however caused, surface tension would tend to promote reduction in the area of the cercus or other structure.

Teratological failure of the segments of the left cercus to fuse has been noted in *Metoligotoma extorris* (Davis 1938); this probably resulted from failure to separate cleanly from the exuvium. A regular failure to fuse would represent an example of neoteny, and a definite contradiction to Dollo's 'Law'.

I am indebted to Mr. E. S. Ross, of the University of California, for the suggestion that the larval setae retain their position when the segments of the left cercus fuse. No exact study of the chaetotaxy has been made, but the setae of the left cercus of the adult male in *Notoligotoma*, *Metoligotoma* and *Anisembia* certainly seem to be very dense at the place where the larval second segment has been wholly or partly resorbed.

Codification of Characters, Figs. 1-4.

Unless annotated, males winged; ± W, winged and wingless forms of male known; —W, males wingless.

R_4, R_5, veins distinct; $R\underset{4+5}{—}$, vein simple; $R_4 \rightarrow R\underset{2+3}{—}$, apparent secondary attachment of R_4 to anterior branch of sector; $\left.\begin{matrix} R\underset{4+5}{—} \\ \hline R_4, R_5 \end{matrix}\right\}$, R_{4+5} simple in forewing, forked in hindwing; 2 M, media regularly forked, simple by anomaly. 1-2M, media usually simple, forked in one or more wings by venational aberrations of moderate frequency; 1M, media regularly simple.

3Cu, cubitus with more than two branches; 2Cu, cubitus with two branches.

..... after any vein represents weakening or partial obsolescence; 2Cu.... indicates that only the anterior branch (Cu_{1a}) is weakened, as the stem (Cu_{1b}) is always strong.

MD!, mandibles greatly over-developed. HMT0, HMT1, HMT2, hind metatarsal bladders 0, 1 or 2. HMT(1-2), medial bladder very small.

$\overline{10}$, tenth abdominal tergite entire; $\overline{\overline{10}}$, divided, with processes of hemitergites small; 10L, 10R, divided, with processes of hemitergites well-developed; 10L, 10R...., divided, with processes prominent, but with suture between hemitergites obsolescent proximally.

10LP(A), process of left hemitergite with a terminal hook or claw; 10LP(B), with a non-terminal lateral or dorsal lobe; 10LP(B...), lateral or dorsal lobe weak; 10LP(C), process of left hemitergite slightly expanded and obliquely truncate terminally; 10LP(X), left hemitergite with a blunt dorsal inner protuberance, but with main process simple.

$10RP_1$, $10RP_2$(X), right hemitergite with an elongate posterior process and an inner ventral flap-like process. $10RP_2$(A), right hemitergite with an inner subelliptical flap; $10RP_2$(B), with a forwardly-directed rod or hook on inner margin; (cf. (A) or cf. (B), approximating to typical form as above); $10RP_2$(C), with a membranous, horizontal, inwardly-directed process.

LC_1, LC_2, RC_1, RC_2, first and second segments of left and right cerci elongate-cylindrical, without nodules; LC_1[A], first segment of left cercus weakly clavate; LC_1(A), more strongly clavate; LC_1(B), with two inner lobes (LC_1[B], inner lobes weak); LC_1(C), with a narrow forwardly-directed hook; *, echinulate; **, echinulate, teeth very strong, sharp; —*, secondary loss of nodules; $\overline{LC}$, two segments of left cercus fused ($\overline{LC}$(A), remains of second segment a terminal incurved extension of first; $\overline{LC}$(B), a distal external protuberance of first). RC_1(A), first segment of right cercus squat.

$\overline{LCB}$, 'left cercus-basipodite' composite (apparently including left half of larval tenth sternite); LCB(A), structures at base of left cercus complex, with the true cercus-basipodite and the supposed left half of the larval tenth sternite distinct, both produced to processes.

RCB!, right cercus-basipodite enlarged; (RCB), right cercus-basipodite suppressed, probably by fusion to cercus.

Distribution: The recent members of the Order seem to be confined to warm countries, extreme ranges being represented by the Crimea and South-east Tasmania. Some species are recorded from dry regions, especially in the Sonoran and Australian regions and in parts of Africa. Although little is at present known of the ecology of the Order, it appears that its members are 'drought-evading' rather than 'drought-enduring', to borrow the plant ecological terms in a somewhat-altered sense. For

instance, the Sonoran species retreat deep into cracks in the soil during the dry season.

With regard to migration of ancestral lines in the past, it seems fairly evident that the further the migration in space, the greater is the structural modification; members which have failed to migrate, or have become geographically fixed at some point of the migration route, seem to have evolved less rapidly than those which have migrated further. As a general assumption, it is supposed that the more recent migration routes have been directed away from the tropics, especially in the colonization of the Australian and Sonoran regions. The Miocene species *Clothoda florissantensis* occurred in Colorado, but it is assumed that its descendants, if any, were driven south by the Pleistocene cold, and that the present Sonoran species have more recently migrated north, either by Central America or by the Antilles.

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Krauss, H. A., 1911.—Monographie der Embien. *Zoologica*, Hft. 60, Bd. 23 (Stuttgart).
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Corrigenda.

Part xv.

Page 183, line 13 from bottom, *for* specimen, *read* species

Page 190, second line of dichotomy 3, *for* smaller, less than ten, *read* smaller, more than ten

Part xvi.

Page 327, line 24, *for* synonyms, *read* synonymous.

Part xviii.

Page 384, line 6 from bottom, *for* subspecies, *read* species

NITROGEN FIXATION AND CELLULOSE DECOMPOSITION BY SOIL MICROORGANISMS. I.

AEROBIC CELLULOSE-DECOMPOSERS IN ASSOCIATION WITH AZOTOBACTER.

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(Two Text-figures.)

[Read 27th November, 1940.]

Introduction.

Although the study of the cellulose-decomposing bacteria has made great progress during the two last decades, the biochemistry of these organisms, and especially the aerobes, still remains incompletely understood. An important phase of this problem is the association between cellulose-decomposing and nitrogen-fixing bacteria which may enter into a symbiotic relationship—a phenomenon which has often been credited with great importance in the cycles of nitrogen and carbon in nature, and particularly in the soil, but which has chiefly been studied by means of impure cultures or total soil populations. Most of the literature in question has been reviewed elsewhere (Jensen, 1940); a few additional papers deserve mention.

McBeth (1911) reported fixation of 8 to 11 mgm. N per 500 ml. solution with 0·1% $(NH_4)_2SO_4$ and 0·2% cellulose, inoculated with *Azotobacter* and cellulose-decomposing bacteria. This appears dubious in view of the high initial content of NH_4–N, some of which might also have been lost during incubation by evaporation from the alkaline control medium, which apparently was only analysed at the end of the experiment. (For instance, McBeth's Table 3 shows 93–94 mgm. N in sterile controls, 102–104 mgm. in cultures. The theoretical N-content of the original medium should, according to its composition, be 106·1 mgm.!)

Tuorila (1928) found gains of 7–8 mgm. N per gm. decomposed cellulose in aerated medium inoculated with soil. The gains decreased with increasing additions of NH_4–N.

Vartiovaara (1938) found only small or insignificant gains of N in combined cultures of *Azotobacter* and cellulose-decomposing fungi under aerobic conditions, but considerable gains in cultures intermittently deprived of oxygen. Similar results were found with fungi + *Clostridium pasteurianum*, and still larger fixations were achieved by fungi + impure cultures of clostridia. Unfortunately the gains of N were not expressed in terms of weight of cellulose destroyed.

Nitrogen-fixing bacteria might derive nutrients from cellulose in several ways; for instance: (*a*) by intercepting the intermediate breakdown products of the cellulose, formed by extracellular enzymes of the cellulose-decomposing organisms; (*b*) by utilizing organic end-products of the metabolism of these organisms; and (*c*) by utilizing their products of cell autolysis. (If the products of nitrogen fixation were in their turn utilized for cellulose decomposition, the association would be an example of real "symbiosis", otherwise of "metabiosis".)

Obviously the metabolism of the cellulose-decomposers is the crucial point of the whole problem. Leaving aside, for the present, the small separate group of more or less strictly anaerobic and often thermophilic spore-forming bacilli which produce large amounts of organic acids and alcohols from cellulose, we shall briefly survey the main

groups of cellulose-decomposing microorganisms and their metabolic products. (For general references, see Winogradsky, 1929, and Waksman, 1932.)

1. *The genus Cytophaga* (Winogradsky, 1929): strictly aerobic organisms of uncertain systematic position and a characteristic morphology and life cycle (Hutchinson and Clayton, 1919; Stapp and Bortels, 1934). They attack no other carbon compound than cellulose, which is partly transformed into an alkali-soluble mucilage and appears to be directly oxidized without previous cleavage of the molecules. Hutchinson and Clayton (1919) stated that organic acids (butyric?) were formed in amounts of about 7% of the decomposed cellulose, but Winogradsky (1929) and Imshenetskij and Solntseva (1936) were unable to detect any organic by-products other than the mucilage. Imshenetskij (1938) found "traces" of reducing sugars in old cultures deprived of oxygen (autolysis products?). Walker and Warren (1938) found about 20% of the decomposed cellulose transformed into mucilage, which gave xylose on acid-hydrolysis and appeared resistant to bacterial but not to fungal attack; small amounts of a non-volatile acid and a non-reducing carbohydrate were found besides the mucilage. Bucksteeg (1936) found the metabolic products of *Cytophaga* unserviceable for *Azotobacter*.

2. *The genus Cellvibrio* (Winogradsky, 1929).—This group is closely related to the familiar genus *Vibrio*, only differing by the capacity of attacking cellulose and the often poor growth in routine media. It appears doubtful whether the "cellvibrios" of Winogradsky (1929), Stapp and Bortels (1934), and others, belong to a genus different from the "vibrios" of Kalnins (1930), Snieszko (1934), and others. The little known genus *Cellfalcicula* Winogradsky (1929) appears very similar except for a slight difference in morphology. The bacteria of this group are obligate aerobes and produce a cellulose-splitting ectoenzyme as shown by the formation of clear zones on cellulose-agar. Winogradsky (1929), Kalnins (1930), and Imshenetskij and Solntseva (1936) found no organic by-products in normal cultures, but Kalnins (1930), Itano and Arakawa (1931) and Imshenetskij (1938) detected the formation of reducing sugars in cultures deprived of oxygen. Snieszko (1934) found no reducing sugars, but "small amounts" of acetic and "traces" of lactic acid (his Table 2, indeed, shows as much as 0·11 gm. acetic and 0·20 gm. lactic acid from 0·376 gm. cellulose; misprint?). Gray (1939) found production of glucose from starch, but not from cellulose.

3. *Aerobic spore-forming bacteria.*—Organisms of this group, which also frequently grow badly in ordinary media, were first found by McBeth et al. (McBeth, 1916). *Bac. latvianus* Kalnins (1930) was stated to produce small amounts of volatile acid. Simola (1931) found that his *Cellulobacillus myxogenes* transformed about 10% of the decomposed cellulose into formic and acetic acid, besides producing traces of alcohol and lactic acid, some unidentifiable non-volatile acid, and certain protein-like excretion compounds. Cellobiose and glucose were identified as intermediate products. Zarembska (1936) found a similar production of volatile acids and no reducing sugars in a closely related organism. Another species (Horowitz-Wlassowa, 1936) produced neither aldehydes, oxy-acids nor reducing sugars.

4. *Aerobic non-spore-forming bacteria* (*Cellulomonas* Bergey et al., 1939).—A large number of more or less strictly aerobic bacteria may decompose cellulose, as first shown by Kellerman, McBeth et al. (summarized by McBeth, 1916). They form a heterogeneous collection, being mostly not specialized in their action on cellulose, and differing widely in morphology and cultural requirements. The justification for a separate genus *Cellulomonas* seems disputable. Their mode of action on cellulose is incompletely known. The many organisms described by McBeth (1916) were stated to grow feebly under anaerobic conditions and to produce acid from several sugars; unfortunately this test did not include cellulose. Bradley and Rettger (1927) and Kalnins (1930) found that some of them produced acid from cellulose in solutions of peptone or digested casein. The latter author isolated two species, *Bact. bosporum* and *Bact. protozoides*, that produced glucose from cellulose, especially when deprived of oxygen, and to a lesser extent at supraoptimal temperatures. Groenewege (1920) found glucose as intermediate product in a somewhat inadequately described aerobic organism. Rubentschick

(1928) mentions two unidentified bacteria that produced no organic acid or reducing sugars. A typical facultative anaerobe was isolated by Dubos (1928), but its metabolic products were not studied. Horowitz-Wlassowa (1936) described a somewhat similar organism (*Bact. cellulosolyticum flavum*) which produced no oxy-acids, aldehydes or reducing sugars, but certain other soluble organic compounds oxidizable by chromic acid.

5. *Myxobacteria.*—Members of this group (to which *Cytophaga* is possibly related) have only in very recent years been known to decompose cellulose. Krzemieniewski (1937) and Imshenetskij and Solntseva (1937) found no acids, alcohols or reducing sugars, but the first author noticed certain pectin-like compounds that gave reducing sugars on hydrolysis with acid.

6. *Actinomycetes.*—Many species of this group are capable of cellulose decomposition, but the biochemistry of this process has been almost completely neglected. Rubentschick (1928) found no organic acids or sugars in the one species studied by him.

7. *Fungi.*—A vast number of fungal species are known to decompose cellulose, many of them very actively, but here, too, our knowledge of their final and intermediate products is remarkably limited. *Chaetomella horrida* produces oxy-acids from cellulose, according to Söhngen (1913), who also mentions this phenomenon in many other cellulose-decomposing organisms, without specifying their identity. Heukelikian and Waksman (1924) found that *Penicillium* and *Trichoderma* transform cellulose quantitatively into carbon dioxide, water, and cell substance. Skinner (1930) observed, by qualitative tests only, that a sterile mycelium, but not *Trichoderma*, produced substances that support growth of *Azotobacter*. *Sporotrichum carnis*, according to Vartiovaara (1935), produces no sugar from cellulose in normal cultures, but does so under the influence of antiseptics or oxygen-starvation. In a *Sterigmatocystis*, Horowitz-Wlassowa (1936) found no aldehydes, oxy-acids or reducing sugars, but large amounts of certain other soluble carbon compounds; the cultures were quite old when analysed, and it is possible that these compounds represent autolysis products. According to Bucherer (1933), fungal mycelium itself may contain certain constituents utilizable by *Azotobacter*.

Symbiosis between cellulose-decomposers and nitrogen-fixers obviously depends not merely on the organic by-products of the former organisms, but also on their ability to use the nitrogen fixation products as sources of nitrogen. This problem has not been studied in much detail. Sanborn and Hamilton (1929) stated that cellulose decomposition by an *Actinomyces* and two *Cellulomonas* was stimulated by *Azotobacter*. Skinner (1930) largely failed to confirm this with *Cytophaga*, *Cellvibrio*, and two fungi. Kalnins (1930) found various unspecified bacteria unable to utilize the nitrogen fixed by *Azotobacter* (by qualitative tests only), and Bucksteeg (1936) made the same observation with *Cytophaga*. Bucherer (1933) found *Azotobacter*-substance well utilized by *Aspergillus* and *Penicillium*, of which particularly the former is not a very active cellulose-decomposer.

From our survey it appears that indisputable proof of nitrogen fixation in combined cultures of one cellulose-decomposing and one nitrogen-fixing organism has been given only by Vartiovaara (1938), whose work was confined to fungi, and possibly by Krishna (1928), who also had pure cultures of fungi only, and in whose data the gains of N look suspiciously small in comparison with the original N-content, especially of the sand media. Secondly it appears that formation of organic acids from cellulose is widespread but inconstant and often slight, and that reducing sugars generally tend to accumulate when the normal course of the metabolism is disturbed by lack of oxygen, high temperature, or antiseptics. Partial nitrogen starvation, which might obtain where the cellulose-decomposers have to depend on the activity of associated nitrogen-fixers, might have a similar effect, with the consequence that larger amounts of breakdown products would be available for interception by the latter group of organisms. Under such conditions it is also possible that by-products like acids or alcohols would be formed more copiously than in normally-fed cultures, or that such compounds might be formed by organisms which do not normally produce them.

With the exception of the important contributions of Bucksteeg (1936) and Vartiovaara (1938), both dealing with only a few specific types of organisms, most work on the problem has been either tentative or incidental to other studies on cellulose decomposition or nitrogen fixation. A systematic investigation of the main groups of cellulose-decomposing microorganisms in their relation to nitrogen fixation has therefore been carried out. The general results obtained with the aerobic types of organisms are presented here. Experiments with anaerobes will follow.

Methods.

Isolation of cellulose-decomposing bacteria.—Crude cultures were mostly obtained by placing strips of filter paper upon a layer of moist soil in a Petri dish and incubating at 28–30°C. When decomposition became visible, a small amount of decayed paper was emulsified in sterile water, and plate cultures on cellulose agar were prepared therefrom. Colonies showing clear zones on cellulose agar were transferred to strips of filter paper in nutrient solutions, and the process repeated until pure cultures were obtained. Some strains were isolated by direct plating from soil with addition of straw.

The agar medium used for isolation contained: precipitated cellulose (prepared by the method of Scales as modified by Kalnins, 1930), 0·5%; $(NH_4)_2SO_4$ 0·1%; K_2HPO_4 0·1%; $MgSO_4$ 0·05%; NaCl 0·02%; $CaCO_3$ 0·2%; agar 1·0%; sometimes also 1% yeast extract prepared by autoclaving dry yeast with 10 times its amount of water. Finely divided cellulose and a low concentration of agar were found essential for successful isolation, especially of *Cytophaga*.

The general basal medium for cultivation was a solution of 0·1% K_2HPO_4, 0·05% $MgSO_4$, and 0·02% NaCl. Various sources of N were added: (*a*) 0·05% $NaNO_3$; (*b*) 0·1% $(NH_4)_2SO_4$ + 0·2% $CaCO_3$; (*c*) 0·1% glycine, asparagine, Na-asparaginate, or peptone; (*d*) 1·0% yeast extract, with or without extra addition of $NaNO_3$, $(NH_4)_2SO_4$, and $CaCO_3$. The media were used in test tubes with strips of filter paper (Whatman No. 1) about two-thirds immersed in the solution. Utilization of sugars, etc., was tested in basal solution with $NaNO_3$ and 1·0% organic compound to be tested. Fermentation tests were made in basal medium with 1% yeast extract and 1% carbohydrate. Diastatic action was tested in starch agar as well as solution. Söhngen's (1913) test for oxy-acids was made on strips of filter paper impregnated with MnO_2 and placed on agar plates with $NaNO_3$ or yeast extract. Growth was also tested on ordinary nutrient agar and broth, potato, and soil extract agar with 1% glucose.

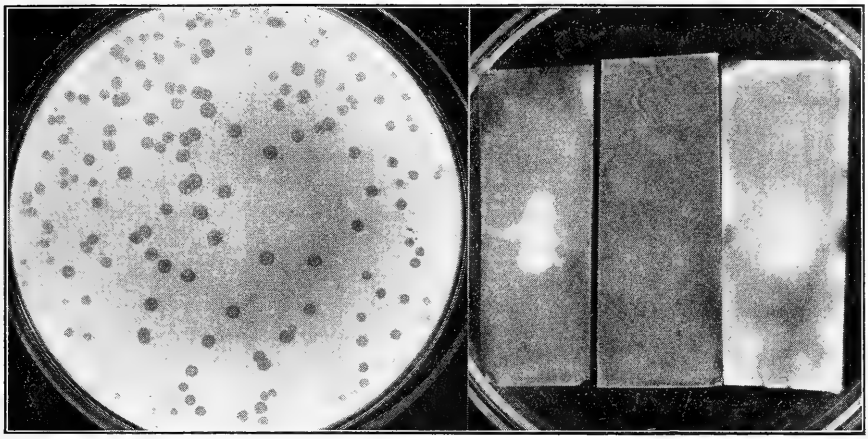
One strain of *Azotobacter chroococcum*, of normal N-fixing capacity (10–14 mgm. N per gm. of glucose), was used throughout the work. A strain of *Az. Vinelandii* was tested occasionally.

All cultures were incubated at 28–30°C. unless otherwise stated.

Nitrogen was determined by the Kjeldahl method, with K_2SO_4 and selenium as catalysts, and digestion for 2 hours after clearing; titration took place in CO_2-free solution, with methyl red and 28/n H_2SO_4 and NaOH.

Descriptions of the Cellulose-decomposing Bacteria.

1. *Cytophaga.*—Six strains were isolated, two (G and F) from soils from the University grounds, the others from wheat soils. Contrary to many statements in the literature, isolation of the cytophagae succeeded readily by repeated plating on cellulose-agar, where they produce no regular colonies, but round transparent plaques gradually covered with yellow mucus (Fig. 1). All strains, the chief characters of which are listed in Table 1, conform to the general definition of *Cytophaga*. Morphologically they appear as long, slender, tapering, somewhat flexible rods which gradually (except in one strain) develop into deeply staining "microcysts". No growth takes place in any cellulose-free medium. Cellulose decomposition starts at the level of the solution, where the paper is softened and transformed into yellow mucus. Strains G, R, and 25 seem to conform to the type species, *Cyt. Hutchinsoni* (syn. *Spirochaeta cytophaga* Hutchinson and Clayton, 1919). Strain F differs mainly by its very pale pigment, and strain 8 by its small size and lack of microcysts. Strain 81 is somewhat similar



1 2

Fig. 1.—Plate culture of *Cytophaga* R on cellulose-agar (10 days, 28-30°C.).
Fig. 2.—Söhngen's reaction: reduction of MnO_2 by oxy-acids, 6 days, 28-30°C. Left, *Corynebact.* 3; centre, Control, sterile; right, *Corynebact.* Va.

to *Cyt. ellipsospora* Imshenetskij and Solntseva (1936), but utilizes no other N-compounds than ammonia and aspartic acid; it also produces less mucilage than the others. Upon the whole, however, the differences between the strains are not so great that it seems advisable to separate them into definite "species".

TABLE 1.
Description of strains of Cytophaga.

	G	R	25	8	F	81
Vegetative cells	0·3–0·5 × 2·5–7·0μ	0·3–0·5 × 2·5–6·0μ	0·3–0·4 × 3·0–6·0μ	0·3–0·4 × 1·8–4·0μ	0·4–0·5 × 2·5–6·0μ	0·2–0·5 × 2·5–6·0μ
Microcysts	Spherical, 1·0–1·2μ	Spherical, 1·0–1·3μ	Spherical, 1·0–1·2μ	Absent	Spherical, 1·0–1·3μ	Oblong, 0·7–0·8× 1·0–1·4μ
Pigment	Ochre-yellow	Ochre-yellow	Light yellow	Ochre-yellow	Pale yellow	Dull orange
Cellulose decomposition with:						
$NaNO_3$	good	good	good	good	good	nil
$(NH_4)_2SO_4$	good	good	good	good	good	good
Glycine	nil	nil	nil	nil	nil	nil
Asparagine	scant	scant	fair	fair	fair	nil
Na-asparaginate	fair	fair	scant	good	fair	scant
Peptone	fair	fair	fair	fair	nil	nil
Cellulose decomposition at:						
6–8° C.	nil	nil	nil	nil	nil	nil
15° C.	slow	slow	nil	slow	nil	slow
18–20° C.	fair	fair	slow	fair	nil	fair
28–30° C.	rapid	rapid	rapid	rapid	rapid	rapid
37° C.	rapid*	rapid*	nil	nil	rapid	rapid

* Variable.

All strains are strictly aerobic; I have not been able to confirm the statement of Imshenetskij and Solntseva (1936) that decomposition may take place under restricted access of oxygen (paper totally immersed in solution). Under these conditions the attack does not start until the paper has reached the surface owing to evaporation. Reducing substances were found neither in normal cultures nor in tubes sealed with paraffin wax and incubated for 6–8 weeks, and no acid reaction developed in cultures with nitrate or peptone. Söhngen's test for oxy-acids was negative.

2. *Cellvibrio.*—Five strains were isolated, one (17) from a wheat soil, the others from soil of the University grounds. On cellulose-agar they produce small, opaque, white colonies surrounded by clear zones, and in liquid media they show a characteristic growth (cf. Kalnins, 1930, et al.), causing first a faint turbidity and then, after 2–3 days, rupture of the paper strip at the level of solution. Morphologically they are much alike: small, non-spore-forming, Gram-negative rods, 0·4–0·6 × 1·0–2·5μ, very actively motile, except strain G3 which showed only a few motile individuals. Curved cells of the typical *Vibrio*-shape were most prominent in strain 17; the others appeared mainly as straight rods with pointed ends, reminiscent of *Cellfalcicula* Winogradsky (1929). It is really disputable whether these two groups should be regarded as separate "genera". Growth is very scant and uncharacteristic on nutrient agar and broth, absent on potato. All grow fairly well on glucose-soil extract-agar, strains G1, G2, and 17 producing a moist, whitish growth, and G3 and G4 a semi-transparent growth of gum-like consistency. On starch-agar the growth of the first three is heavy and yellowish-white, of the two last very scant. Various other characters are seen in Table 2.

TABLE 2.
Description of Cellvibrio-*like organisms.*

	G1	G2	17	G3	G4
Cellulose decomposition with:					
$NaNO_3$	rapid	rapid	rapid	rapid	rapid
$(NH_4)_2SO_4$	rapid	rapid	rapid	rapid	rapid
Glycine	nil	nil	nil	nil	?
Asparagine	slow	nil	nil	slow	nil
Na-asparaginate	fair	fair	slow	fair	fair
Peptone	slow	slow	?	slow	nil
Yeast extract	fair	fair	fair	fair	slow
Utilization of:					
Glycerine, Mannite, Xylose, Arabinose	nil	nil	nil	nil	nil
Glucose	good	good	good	fair	good
Saccharose	good	good	fair	fair	fair
Lactose	nil	fair	fair	nil	nil
Inulin	good	nil	nil	nil	nil
Starch	fair	good	good	scant	scant
Diastatic action, plate	strong	strong	strong	nil	nil
Do., solution	strong	strong	strong	fair	fair
Reduction of NO_3 to NO_2	strong	weak	nil	strong	strong
Growth at:					
5° C.	slow	slow	slow	slow	slow
15° C.	fair	fair	fair	fair	fair
28° C.	rapid	rapid	rapid	rapid	rapid
37° C.	nil	nil	nil	fair	fair

Unlike *Cytophaga*, the cellvibrios utilize glucose, saccharose and starch more or less readily, sometimes also lactose or inulin. They are also better adapted to low temperatures than *Cytophaga*. Strains G1, G2 and 17 are very similar to *Cellv. vulgaris* Stapp and Bortels (1934), except that they form a very faint (often invisible) yellow pigment on the paper exposed to the air. Strains G3 and G4 differ slightly by their weak diastatic effect, tolerance of higher temperature, and more copious formation of polysaccharide, as shown by their very slimy growth in sugar solutions and soil-extract agar. No growth takes place in the anaerobic jar, but paper submerged in nutrient solution is attacked, although very slowly. No acid is produced from any carbohydrate in nitrate-solution or from cellulose in any medium, except, of course, in $CaCO_3$-free solution with $(NH_4)_2SO_4$, where an acid reaction (pH 5·6–6·0) develops owing to selective absorption of the ammonium. In this medium strain G1 and G2 produced after

3 weeks small amounts of substances that reduced Fehling's solution. Otherwise no reducing sugars were found in normal cultures, even after 4 months, but all strains produced such compounds in paraffin-sealed tubes after 5–6 weeks (cf. Kalnins, 1930). Some polysaccharide seems to be produced in cellulose-cultures, where the solution after 2–3 months became slightly viscous and gave a small flocculent precipitate with HCl-alcohol. Söhngen's reaction is negative.

3. *Aerobic spore-forming and non-spore-forming bacteria* (*"Cellulobacillus"* and *"Cytobacter"*).—Two non-spore-forming cellulose-decomposers, "R" and "Co", were isolated from wheat soils, and two spore-formers, "G" and "43", from University grounds soil and pasture soil, respectively. (Two other spore-formers were isolated, but died out after a few transfers). Their chief characters are seen in Table 3.

TABLE 3.

Description of non-spore-forming and spore-forming cellulose-decomposing bacteria.

	Bact. R.	*Bact.* Co.	*Bacillus* 43.	*Bacillus* G.
Vegetative cells	Rods often curved, 0·5–1·0 × 2·5–5·0μ	Straight rods, 0·5–0·6 × 1·5–2·5μ	Slightly curved rods, at sporulation spindle-shaped, 0·4–0·6 × 1·5–2·6μ	Straight rods, spindle-shaped at sporulation, 0·6–1·2 × 2·4–4·5μ
Spores	absent.	absent.	Subterminal, or central, oval, 0·5–0·8 × 1·2–1·6μ	Subterminal, oval, 0·7–1·0 × 1·2–2·0μ
Motility	none	none	none	?
Gram	–	–	–	variable
Cellulose decomposition with:				
$NaNO_3$	nil	nil	nil	nil
$(NH_4)_2SO_4$	nil	nil	nil	scant
Glycine	nil	nil	nil	nil
Asparagine	scant	nil	nil	scant
Na-asparaginate	nil	nil	nil	nil
Peptone	scant	scant	nil	nil
Yeast extract	fair	fair	fair	fair
Acid in:				
Glycerine	–	–	–	–
Mannite	–	–	–	–
Xylose	–	–	–	(+)
Arabinose	–	–	(+)	(+)
Glucose	–	+	–	?
Saccharose	–	–	–	–
Lactose	–	–	?	?
Inulin	–	–	–	–
Starch	–	+	–	–
Cellulose	–	+	–	–
Diastatic action, plate	+	–	+	+
Do., solution	+	+	+	–
Söhngen's reaction	–	+	–	–
Reduction of nitrate	+	+	+	+
Cellulose decomposition at:				
9–10° C.	nil	nil	nil	nil
15° C.	nil	very slow	very slow	very slow
28–30° C.	fair	fair	fair	fair
37° C.	fair	fair	fair	nil

They are strictly aerobic, do not grow in the anaerobic jar, and attack submerged paper very slowly. Otherwise the paper is attacked in the same manner as by *Cellvibrio*, but less rapidly. The growth on nutrient agar and broth, soil-extract agar and potato is very scant or absent. *Bac.* G alone produces a heavy, colourless, semi-transparent, gummy growth on starch agar with $NaNO_3$ or yeast extract. Reducing sugars are formed from starch, and from cellulose in sealed but not in open tubes. *Bact.* Co produces acid from cellulose (oxy-acid as shown by Söhngen's reaction), and from glucose and starch, while the fermentative powers of the other isolates are only weak. *Bact.* R bears some resemblance to *Cytobacter polonicum* Gutgisser (1936), but unlike this it is unable to utilize nitrate, ammonia, or simple amino-compounds; this is common to all except *Bac.* G, which strongly resembles *Cellulobacillus myxogenes* Simola (1931) and *Cell. varsaviensis* Zarembska (1936), except that it is almost non-motile (only a few cells show vibratory movement), has less fermentative power, and does not produce acid from the cellulose. The remarkably small *Bac.* 43 does not seem identifiable with any hitherto described species.

4. *Facultative aerobic, non-spore-forming bacteria.*—This group, which largely conforms to the genus *Cellulomonas*, includes an authentic strain of *Cell. biazotea* (McBeth, 1916), received from the Biological Branch, Dept. of Agriculture, N.S.W., and three *Corynebacterium*-like organisms. One of these (*Cor.* 3) was isolated from wheat soil, the others (*Cor.* Va and Vb) from a crude culture of cellulose-decomposers from leaf compost (kindly supplied by Mr. J. M. Vincent, School of Agriculture, University of Sydney).

Morphologically, *Cell. biazotea* appeared as short, straight rods, non-motile and of unstable Gram-reaction. Strains 3 and Vb were typical small corynebacteria: in young cultures somewhat irregularly shaped, slender, non-motile, Gram-positive rods in angular arrangement (strain 3: 0·5–0·6 × 1·0–2·0μ; strain Vb: 0·4–0·5 × 2·0–4·0μ; later the cells become very short to coccoid). *Cor.* Va was similar to *Cor.* 3, but actively motile in broth culture (cf. Topping, 1937, on motile soil corynebacteria). Cellulose is attacked as by the cellvibrios, but in suitable media even more intensely, especially below the surface of the liquid; in accordance herewith, submerged paper is readily attacked, and a slow but definite cellulose decomposition takes place in the anaerobic jar. Other characters are given in Table 4.

TABLE 4.

Description of cellulose-decomposing Corynebacteria, and Cell. biazotea.

	Cell. biazotea.	*Cor.* 3.	*Cor.* Va.	*Cor.* Vb.
Motility	none	none	motile in broth	none
Gram	variable	positive	positive	positive
Growth on:				
Nutrient agar	abundant, slimy, light yellow	abundant, slimy, yellow	abundant, pasty, yellow	fair, white to pale yellow, sticky
Nutrient broth	turbid, white sediment	turbid, white sediment	turbid, white sediment	turbid, white sediment
Potato	good, yellow	good, yellow	good, yellow	very scant, yellow
Growth on cellulose with:				
$NaNO_3$	nil	nil	nil	nil
$(NH_4)_2SO_4$	nil	nil	nil	nil
Glycine	nil	scant	scant	scant
Asparagine	nil	nil	nil	nil
Na-asparaginate	nil	nil	scant	scant
Peptone	fair	fair	fair	fair
Yeast extract	good	good	good	good
Acid in:				
Glycerine	+	+	+	+
Mannite	−	−	−	−
Arabinose	+	+	+	+
Xylose	−	+	+	+

TABLE 4.—*Continued.*
Description of cellulose-decomposing Corynebacteria, and Cell. biazotea.—Continued.

Acid in :				
Glucose	+	+	+	+
Saccharose	+	+	+	+
Lactose	+	+	−	+
Inulin	−	−	−	−
Starch	+	+	+	+
Cellulose	+	+	+	+
Söhngen's reaction (cellulose–MnO_2)	(+)	+	+	+
Diastatic action	strong	strong	strong	strong
Reduction of NO_3	strong	strong	strong	strong
Cellulose decomposition at pH :		(Paper broken after days :)		
5·2	20–30	13	>30	>30
5·7	9	7	7	7
6·1	9	5	7	7
6·4	5	5	4–5	4–5
6·6	6	4	5	4–5
6·9	6	4–5	4–5	2–3
Cellulose decomposition at :				
5° C.			nil	nil
10° C.	nil	nil	very slow	very slow
15° C.	slow	slow	slow	slow
28° C.	rapid (opt.)	rapid (opt.)	rapid } (opt.)	rapid } (opt.)
37° C.	rapid	rapid	rapid }	rapid }

The organisms of this group differ from all the previous ones in their good growth in routine media, their fermentation of a wide range of carbohydrates, and their facultative-anaerobic nature. High-molecular N-compounds seem required; simple amino-compounds are but slightly utilized, and inorganic N not at all (except in the presence of yeast extract, where small amounts of NH_4–N are assimilated, as shown by a separate experiment). Soil extract can be used instead of yeast extract. The resistance to acidity is considerable, cellulose being still attacked at pH 5·2. The fermentative reactions of the 4 isolates are almost identical, including the production of acid from cellulose; Söhngen's test shows rapid and vigorous formation of oxy-acids (Fig. 2). No reducing sugars are produced from cellulose either in open or in sealed tubes (in the latter case probably because these bacteria, being facultative anaerobes, can further ferment the sugar that might arise). *Cor.* Va gave a faint reduction in sealed tubes with addition of toluene.

Cor. 3 seems closely related to "*Cellulomonas*" *fimi*, which has previously (Jensen, 1934) been recognized as a corynebacterium. The other two isolates cannot with certainty be identified with any other adequately described species.

5. *Actinomycetes and fungi.*—Some representatives of these were included for comparison: two species of *Actinomyces*, a *Micromonospora*, a *Trichoderma* (*koningi*?), and an unknown fungus ("P") isolated from University grounds soil and similar to a *Botryosporium*-like fungus previously studied (Jensen, 1930). They all decompose cellulose vigorously with $(NH_4)_2SO_4$, yeast extract or soil extract as sources of N. Oxy-acids are not produced, except perhaps by *Micromonospora* which showed a trace of reaction. Reducing sugars are formed from cellulose in sealed but not in open tubes; upon the whole this seems to be a general property of obligate aerobic cellulose-decomposers other than *Cytophaga*.

Associations between Azotobacter and Cellulose-decomposing Organisms.

The value of cell-substance of *Azotobacter* as a source of N for the cellulose-decomposers was first tested qualitatively by growing all these organisms in basal solution with filter paper and cell-material of *Az. chroococcum*, grown on mannite-agar 8 days 28°C., and added in a quantity corresponding to 0·1% dry matter. Growth was

also tested on agar corresponding to the basal solution, with 2·5% moist substance of *Azotobacter*.

TABLE 5.

Utilization of cell nitrogen of Azotobacter *for cellulose decomposition, and lysis of* Azotobacter*-cells.*

Organism.	Cellulose decomposition.	Cytolysis.	Organism.	Cellulose Decomposition.	Cytolysis.
Cytophaga (6 strains) ..	nil		*Cell. biazotea*	rapid	fair
			Corynebact. 3	,,	,,
Cellvibrio 1	slow	none	,, Va	,,	none
,, 2	,,	,,	,, Vb ..	,,	,,
,, 3	,,	,,			
,, 4	very slow	,,	*Actinomyces* R	fair	strong
,, 17	,,	,,	,, T	,,	,,
			Micromonospora	,,	,,
Bact. Co.	rapid	strong	*Trichoderma*	rapid	,,
Bact. R.	nil	none	Fungus "P"	,,	,,
Bacillus 43	very slow	,,			
,, G	fair	,,			

Table 5 shows that all except *Cytophaga* and *Bact.* R can utilize *Azotobacter*-N, the bacteria of group 4 even very readily, and several show active lysis of *Azotobacter*-cells. These had indeed been killed by the sterilization; but also the N in untreated *Azotobacter*, added aseptically to basal solution with filter paper, was readily utilized by *Cellv.* G2 and 17, and *Cor.* 3 and Vb.

In another series of qualitative tests *Az. chroococcum* and *Vinelandii* were grown on filter paper in solution with 0·2% glucose and the usual salts including Fe, Mo, and $CaCO_3$. After 6–7 days, when a good growth of *Azotobacter* had appeared, the cultures were superinoculated with the cellulose decomposers and incubated further; in no case did more than a trace of cellulose decomposition result. An active "symbiosis" between pure cultures thus cannot be started with *Azotobacter*-N, at least not in amounts so small as the present (cf. Kalnins, 1930). Theoretically, however, all cellulose-decomposers should be able to derive nitrogen from *Azotobacter*; groups 3–5 readily take up the N of its dead cells, and one of its main vital secretion products is aspartic acid (Virtanen and Laine, 1937; Horner and Burk, 1939), which is quite a favourable source of N for *Cytophaga* and *Cellvibrio*. (Spontaneous formation of NH_4–N by *Azotobacter* is hardly to be expected during symbiosis, since this does not take place when the medium contains more than very small amounts of oxidizable organic matter.)

Further qualitative tests showed that *Azotobacter* regularly produced some growth (usually sparse) when introduced into filter paper cultures of practically all cellulose decomposers (cf. Kalnins, 1930, and Skinner, 1930). In the main experiment it was therefore attempted to start symbiosis by supplying a quantity of fixed N sufficient to initiate cellulose decomposition, yet small enough to be rapidly consumed and thus ceasing to interfere with the fixation by *Azotobacter*.

This experiment was made with cultures in large test tubes (20 × 3 cm.) containing 40 c.c. nutrient solution and 0·5 or 1·0 gm. filter paper about two-thirds immersed in the solution which contained, besides the usual salts, 0·01% $FeCl_3$, 0·001% Na_2MoO_4, and 0·25% $CaCO_3$. Nitrogen was added in amounts of 2·5 to 3·0 mgm. per culture, as $(NH_4)_2SO_4$, peptone, or yeast extract. After sterilization, tubes were inoculated with various combinations of organisms and incubated for 4 or 5 weeks. Total N was determined both before and after incubation. In all cultures of cellulose decomposers the paper was attacked quickly, although mostly not to a large extent; growth of *Azotobacter* was visible in these cultures, but, except in a few instances, only as faint dark streaks on the paper or thin rings around the surface of the solution.

Table 6 gives the analytical data, as averages of duplicate cultures unless otherwise stated; the agreement between duplicates was such that differences exceeding 0·3 mgm. N may be regarded as significant. These figures show that:

1. Sterile solutions of $(NH_4)_2SO_4$ show a loss of N, whereas yeast extract solutions remain almost unchanged; the initial N-content has therefore been subtracted from that of the cultures to give the N-balance.

2. *Azotobacter* alone fixes no N in the media employed.

3. None of the cellulose-decomposers absorb significant quantities of N from the atmosphere, although they largely prevent the loss of N from the media.

4. No combination of *Azotobacter* with *Cytophaga* (even crude cultures), *Cellvibrio*, bacteria of group 3, actinomycetes or fungi, fixes a significant amount of N.

5. In association with the bacteria of group 4, and especially *Cor.* 3 and *Cor.* Vb, *Azotobacter* fixes considerable amounts of N; in these cultures also the growth and cellulose decomposition appear more vigorous than in others.

TABLE 6.

Nitrogen fixation in combined cultures of Azotobacter *and cellulose-decomposing organisms.*

Series.	Inoculum.	Total N, mgm.	Gain or loss of N, mgm.
I.	Control at start	2·11	
1·0 gm. paper,	Do. incubated	1·48	−0·63
2·5 mgm. N as	*Az. chroococcum* (single)	1·19	−0·92
$(NH_4)_2SO_4$	*Cellvibrio* G2	1·95	−0·16
Inc. 35 d.	Do. + *Azotobacter*	2·30	+0·19
	Do. + do. + crude culture of cellulose-decomposers	2·10	−0·01
II.	Control at start	2·39	
1·0 gm. paper,	Do. incubated	2·15	−0·24
with 5% yeast	*Az. chroococcum*	1·99	−0·40
extract.	*Bacillus* 13* (single)	2·19	−0·20
Inc. 35 d.	Do. + *Azotobacter*	2·27	−0·12
III.	Control at start	2·66	
1·0 gm. paper,	Do. incubated	1·76	−0·90
3·0 mgm. N as	*Trichoderma*	2·47	−0·19
$(NH_4)_2SO_4$.	Do. + *Azotobacter*	2·88	+0·22
Inc. 35 d.	Do. + do. + crude *Cytophaga*-culture	2·52	−0·14
IV.	Control at start	1·94	
1·0 gm. paper,	Do. incubated (triplicate)	1·38	−0·56
2·5 mgm. N as	*Cellvibrio* G3	1·97	+0·03
$(NH_4)_2SO_4$	Do. + *Azotobacter*	2·11	+0·17
Inc. 35 d.	*Cellvibrio* 17	1·93	−0·01
	Do. + *Azotobacter*	1·97	+0·03
	Cytophaga 8 + *Azotobacter*	1·94	0·00
V.	Control at start	1·92	
1·0 gm. paper,	Do. incubated	1·57	−0·35
2·5 mgm. N as	*Cytophaga* R (single)	1·86	−0·06
$(NH_4)_2SO_4$.	Do. + *Azotobacter*	1·93	+0·01
Inc. 35 d.	Do. + do. + crude *Cytophaga*	1·90	−0·02
VI.	Control at start	1·88	
1·0 gm. paper,	Fungus "P"	1·90	+0·02
2·5 mgm. N as	Do. + *Azotobacter*	1·98	+0·10
$(NH_4)_2SO_4$	*Micromonospora*	1·84	−0·04
Inc. 35 d.	Do. + *Azotobacter*	2·07	+0·19
VII.	Control at start	1·86	
1·0 gm. paper,	Do. incubated	1·82	−0·04
4% yeast extract.	*Corynebact.* 3 (single)	1·84	−0·02
Inc. 35 d.	Do. + *Azotobacter*	2·51	*+0·65*
	Bacillus G + *Azotobacter*	1·94	+0·08
	Trichoderma + *Azotobacter*	1·91	+0·05

TABLE 6—*Continued.*

Nitrogen fixation in combined cultures of Azotobacter *and cellulose-decomposing organisms.*—Continued.

Series.	Inoculum.	Total N, mgm.	Gain or loss of N, mgm.
VIII.	Control at start	1·74	
1·0 gm. paper,	Do. incubated	1·29	−0·45
2% yeast extract,	*Cell. biazotea* (single)	1·84	+0·10
1·25 mgm. N as	Do. + *Azotobacter*	1·91	+0·17
$(NH_4)_2SO_4$.	*Bacillus* G (single)	1·73	−0·01
Inc. 35 d.	Do. + *Azotobacter* (single)	1·17	−0·57
	Corynebact. 3 + *Azotobacter*	3·13	*+1·39*
IX.	Control at start	2·70	
1·0 gm. paper,	*Cell. biazotea* (single)	2·61	−0·09
0·04% peptone.	Do. + *Azotobacter*	3·31	*+0·61*
Inc. 28 d.	*Corynebact.* 3 (single)	2·66	−0·04
	Do. + *Azotobacter*	3·81	*+1·11*
	Do. + *Az. Vinelandii*	4·50	*+1·80*
X.	Control at start	1·92	
1·0 gm. paper,	*Actinomyces* R (single)	2·08	+0·16
2·5 mgm. N as	Do. + *Azotobacter*	1·99	+0·07
$(NH_4)_2SO_4$.	*Actinomyces* T (single)	2·08	+0·16
Inc. 35 d.	Do. + *Azotobacter*	2·00	+0·08
	Cytophaga 25 + *Azotobacter*	2·05	+0·13
	Cytophaga F. + *Azotobacter*	2·10	+0·18
XI.	Control at start	3·38	
0·5 gm. paper,	*Corynebacterium* Va (single)	3·25	−0·13
2·4% yeast extract	Do. + *Azotobacter*	3·80	*+0·42*
(new batch).	*Corynebacterium* Vb (single)	3·53	+0·15
Inc. 28 d.	Do. + *Azotobacter*	4·52	*+1·14*
	Bacillus 43 + *Azotobacter*	3·34	−0·04
	Bacterium R + *Azotobacter*	3·27	−0·11
XII.	Control at start	2·38	
0·5 gm. paper,	*Bacterium* Co. (single)	2·58	+0·20
2% yeast extract.	Do. + *Azotobacter*	2·44	+0·06
Inc. 33 d.	*Cellvibrio* G1 + *Azotobacter*	2·27	−0·11
	Micromonospora (single)	2·26	−0·12
	Do. + *Azotobacter*	2·42	+0·04
XIII.	Control at start	2·10	
0·5 gm. straw	*Cellvibrio* G2 + *Azotobacter*	2·07	−0·03
(H_2O-extr.), on agar	*Bacillus* G + do.	2·07	−0·03
medium, 1·0 mgm. N as	*Micromonospora* + do.	2·05	−0·05
$(NH_4)_2SO_4$.	*Actinomyces* R + do.	2·04	−0·06
Inc. 36 d.	*Trichoderma* + do.	2·00	−0·10
24–27° C.			
XIV.	Control at start	2·60	
0·5 gm. paper,	*Cellvibrio* G2 + *Azotobacter*	2·52	−0·08
on agar medium,	*Cytophaga* 25 + do.	2·52	−0·08
2·0 mgm. N as	*Trichoderma* + do.	2·82	+0·22
$(NH_4)_2SO_4$.			
Inc. 36 d.			
24–27° C.			

* This isolate died out after a few transfers.

Two additional series of experiments were made (last section of Table 6). In the first, wheat straw from which the constituents directly available to *Azotobacter* had been removed by extraction with hot water (Jensen, 1940) was used as a cellulosic material possibly more easily attacked by the organisms under investigation (cf. Norman, 1937). Portions of 0·5 gm. dry, finely ground straw and 0·1 gm. $CaCO_3$, sterilized separately, were placed on the surface of 50 c.c. agar medium in 250 c.c. flasks; the agar contained the usual salts and 1·0 mgm. N as $(NH_4)_2SO_4$ per flask. The second series was identical except that filter paper was used instead of straw. *Trichoderma*

made a fair growth in both series, the other organisms almost none, and no nitrogen was fixed.

The whole experiment shows clearly that the more or less highly specialized cellulose-decomposers (*Cytophaga*, *Cellvibrio*, "*Cellulobacillus*", etc.), as well as fungi and actinomycetes, do not form organic metabolic by-products or autolysis-products in such quantities as to serve for a discernible N-fixation by *Azotobacter*. Neither does *Azotobacter* seem to intercept the intermediate breakdown products of cellulose, even in solution cultures with a fairly high layer of liquid which should encourage the production of reducing sugars. The ability to "feed" *Azotobacter* from cellulose seems, apart from the obligate anaerobes, to belong exclusively to the facultative anaerobes of the Kellerman-McBeth group, an outstanding character of which is their ability to utilize *Azotobacter*-N readily and to ferment cellulose under production of organic acids which are favourable sources of energy for *Azotobacter*. (*Bact.* Co, indeed, also forms such compounds, but these seem unsuitable for *Azotobacter*.) In cases where N-fixation has been recorded by *Azotobacter* in combination with impure cultures of cellulose-decomposers, either in solution cultures or in the soil (Jensen, 1940) we must be justified in concluding that either obligate anaerobes or else bacteria of the present type have been active.

The nature of the metabolic products, the quantitative relation between cellulose decomposition and N-fixation, and the influence of environmental factors will be discussed in a subsequent paper.

Summary.

Various groups of aerobic cellulose-decomposing microorganisms, viz., 6 strains of *Cytophaga*, 5 of *Cellvibrio*, 3 of *Corynebacterium*, 4 of unidentified spore-forming and non-spore-forming bacteria, besides fungi and actinomycetes, were isolated and grown in combination with *Azotobacter* in media with cellulose as a source of energy. *Azotobacter* was able to fix nitrogen only in association with the corynebacteria and *Cellulomonas biazotea*. Unlike the "typical" cellulose decomposers, these organisms are facultative anaerobes, grow well in ordinary media, utilize the nitrogen in *Azotobacter*-substance readily, and decompose the cellulose with the formation of organic acids. Organisms of this type may have been the active agents in cases where nitrogen fixation has been reported by *Azotobacter* in combination with impure cultures of cellulose-decomposers.

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FURTHER INVESTIGATIONS ON NITROGEN-FIXING BACTERIA IN SOIL.

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Introduction.

In an earlier paper (Swaby, 1939) it was shown that waterlogging a soil tends to increase the numbers of *Clostridium butyricum*, and it was suggested that anaerobic nitrogen fixation might occur after heavy rains. It was also found (Jensen, 1940) that considerable amounts of nitrogen may be fixed in waterlogged soil, but apparently chiefly through the activity of *Azotobacter*. The following investigations were designed to test, firstly, how far the development of *Azotobacter* and *Cl. butyricum* could be affected by varying the water content of the soil between a comparatively moist state and saturation point, and, secondly, whether a correlation could be traced between multiplication of *Cl. butyricum* and nitrogen content of the soil. In addition, some supplementary data on the distribution of *Azotobacter* and the possible existence of other nitrogen-fixing bacteria in Australian soils are presented.

1. *Influence of Soil Moisture on Nitrogen-fixing Bacteria.*

The soil used for this investigation was taken from a plot in the Melbourne University grounds: immature grey sandy-loam, of pH 7·2, and containing 0·10% total-N and 1·73% organic carbon.† The plot has been used for growing cereals for a period of years, and has received heavy applications of lime and superphosphate, in recent years also a small quantity of manganese sulphate.

Schofield (1935) pointed out that the air-water relationship of a soil could not be measured by moisture determination alone, and suggested the use of the term pF, which is the logarithm of the capillary tension; this is used as an index of the aeration and water content of the soil in the present study. The filter paper method (Gartner, 1937) was found to give good results up to the sticky point (18% H_2O).

Bacterial counts were made by the methods previously described (Swaby, 1939). Each count was triplicate, i.e., a minimum difference of 80% between counts is necessary for significance.

An experiment was first designed to imitate field conditions after light and heavy rains and their influence on N-fixing bacteria. A bulk sample of soil was collected at the end of the summer, and 4 sub-samples, of approximately 150 gm., were made up to 6, 16, 28 and 38% moisture. Replicate sub-samples were incubated at 22°C. in Petri dishes of 10 cm. diameter, and loss of weight by evaporation was made up periodically by addition of water. Counts of *Azotobacter* and *Cl. butyricum* were made prior to incubation and subsequently at intervals of a few days by removing several cores of soil from each Petri dish and mixing together to form 4 composite samples. The results of these counts are given in Table 1.

* The first section of this work was carried out by the junior author in the Department of Bacteriology, University of Melbourne. The third section was carried out by the senior author, and the second section by both authors in collaboration.

† This abnormally wide C/N ratio was doubtless due to the presence of some material from asphalt road sweepings.

TABLE 1.
Effect of Soil Moisture Content on Azotobacter *and* Clostridium butyricum. (*Depth of soil 2 cm.*)

State of Soil.	Inc. Days.	*Azotobacter* per gm.	Clostridia per gm.		pH.
			Total.	Spores.	
Initial	0	20	470	300	7·3
Moist, aerated, H_2O 6%. pF 3·9..	3	18	400	200	
	8	16	400	300	
	20	13	200	100	6·8
Wet, aerated, H_2O 16%. pF 2·2..	3	24	600	370	
	8	13	300	300	
	20	13	200	100	6·8
Saturated, H_2O 28%..	3	11	800	400	
	8	13	500	200	
	20	13	200	100	7·0
Waterlogged, H_2O 38%	3	20	1,600	330	
	8	20	200	200	
	20	13	300	200	7·0

The numbers of *Azotobacter* showed neither any appreciable increase after prolonged incubation, nor any decline as the soil moisture increased. The counts of *Cl. butyricum* were slightly more variable, and were generally higher in the waterlogged than in the drier samples; in all cases they outnumbered *Azotobacter*. In view of the increase in *Cl. butyricum* observed previously (Swaby, 1939), it would seem that anaerobic conditions were not obtained in the shallow plaques used. This is borne out by the occurrence of *Azotobacter* under all conditions and the fact that many of the clostridia exist as dormant spores.

A second experiment was carried out with the same soil brought to approximately the same pF values, but contained in jars 16 cm. in depth. Hereby the access of air to the bottom of the containers was prevented when the soil was waterlogged, but not when it was moist and crumbly. Otherwise the jars were treated as in the first experiment. The results are set out in Table 2.

TABLE 2.
Effect of Soil Moisture Content on Azotobacter *and* Clostridium butyricum. (*Depth of soil 15 cm.*)

State of Soil.	Inc. Days.	*Azotobacter* per gm.	Clostridia per gm.		pH.
			Total.	Spores.	
Initial	0	7	330	100	7·2
Moist, aerated, H_2O 7%. pF 3·8..	6	7	330	200	
	11	60	266	100	
	28	33	330	300	6·9
Wet, aerated, H_2O 16%. pF 2·2..	6	15	330	130	
	11	60	270	100	
	28	27	330	300	6·8
Saturated, H_2O 25%..	6	47	530	200	
	11	40	270	130	
	28	73	270	300	7·1
Waterlogged, H_2O 38%	6	7	1,000	330	
	11	22	200	140	
	28	33	330	300	7·2

The numbers of *Azotobacter* increased as incubation proceeded, but the numbers at different moisture content show no significant differences, although the numbers at 25% appear highest. The counts of *Cl. butyricum* show no significant increase after prolonged

incubation, and except for two fairly high values in saturated and waterlogged soil there is no obvious increase in their numbers as the pF values fall. The numbers of spores are still high in comparison with those of vegetative cells. The failure of the clostridia to respond to waterlogging and the slight development of *Azotobacter* under moist aerated conditions might possibly be due to the soil being deficient in organic matter available to the bacteria, especially as the sample was collected after a very dry summer. (The soil which previously showed increase in clostridia after waterlogging (Swaby, 1939) was collected in the spring and probably contained carbohydrates from plant residues.) A third experiment was therefore carried out, in which a small quantity of carbohydrate was added to the soil. Deep jars were filled with soil plus 0·2% glucose and made up to 4 different moisture conditions, and bacterial counts were made as before. The results are set out in Table 3.

TABLE 3.
Effect of Soil Moisture and Carbohydrate Content on Azotobacter *and* Clostridium butyricum.

State of Soil.	Inc. Days.	*Azotobacter* per gm.	Clostridia per gm.		pH.
			Total.	Spores.	
Initial	0	5	400	80	7·2
Moist, aerated, H_2O 8%. pF 3·7 ..	3	110	1,100	670	
	8	4,000	640	270	
	15	20,000	1,600	800	
	20	48,000	2,000	1,000	7·0
Wet, aerated, H_2O 14%. pF 2·8 ..	3	100	2,600	2,100	
	8	7,000	3,200	3,000	
	15	60,000	12,000	10,000	
	20	120,000	12,000	10,000	7·4
Saturated, H_2O 20%..	3	90	3,200	3,000	
	8	180	7,700	3,000	
	15	6,700	12,000	12,000	
	20	30,000	14,000	10,000	7·7
Waterlogged, H_2O 24%	3	4	3,100	1,400	
	8	67	7,700	3,000	
	15	2,000	16,000	18,000	
	20	1,000	13,000	14,000	7·2

Azotobacter, as might be expected, showed in all cases a rapid increase from a few to thousands per gm. of soil, but in the waterlogged soil the final numbers were lower and the rate of increase not so rapid. The counts of clostridia showed a similar increase as the incubation proceeded, and their final numbers were highest in the waterlogged soils which smelled of butyric acid; throughout the whole experiment the number of spores was large and quite the reverse of what might be expected. Generally the results are in full agreement with those of Winogradsky (1926). The high counts of *Azotobacter* under wet conditions might be due to surface growth, but the relatively strong increase in clostridia in the aerated soils is less readily explicable. Either the clostridia existed in association with protective aerobes, or else the soil must have contained unknown reducing substances capable of lowering the oxidation-reduction potential.

Under field conditions it is unlikely that the amount of soluble carbohydrate would ever amount to anything like 0·2% glucose. Therefore a fourth experiment was designed to imitate the conditions after the stubble of a four-ton-per-acre crop of oats had been ploughed in: 0·4% very finely ground oaten hay was added to University soil of two moisture conditions—moist aerated, and waterlogged. It was conceivable that the balance between aerobic and anaerobic nitrogen fixers might be influenced by the presence of an oxidizing agent which theoretically ought to favour *Azotobacter* and suppress the clostridia. The only important oxidizing substance naturally occurring in

the soil is manganese dioxide; therefore, 0·5% active MnO_2 was added to both aerated and waterlogged soil with oaten hay. The soils were incubated at 22°C. in 15 cm. deep jars, and bacterial counts made. Table 4 gives the results.

TABLE 4.

Influence of Hay and Manganese Dioxide on Azotobacter *and* Cl. butyricum *in Soil at Different Moisture Content.*

State of Soil.	Treatment.	Inc. Days.	*Azotobacter* per gm.	Clostridia per gm.	
				Total.	Spores.
Initial		0	15	500	400
Moist, aerated, H_2O 11%. pF 3·4.	Control	3	50	500	500
		6	50	500	400
		10	50	1,700	500
	0·4% hay	3	40	500	400
		6	100	700	300
		10	100	1,000	600
	0·4% hay, 0·5% MnO_2	3	40	500	400
		6	60	600	300
		10	75	1,200	800
Waterlogged, H_2O 20% ..	Control	3	20	600	400
		6	60	300	300
		10	60	1,500	800
	0·4% hay	3	600	1,000	400
		6	2,700	1,000	800
		10	14,400	3,200	1,200
	0·4% hay, 0·5% MnO_2	3	38	1,000	400
		6	66	1,000	1,000
		10	100	2,000	2,000

Both under aerated and waterlogged conditions there was a progressive increase in *Azotobacter* and *Cl. butyricum*, and especially in the jars with hay. At 11% moisture the addition of hay increases the numbers of *Azotobacter* and clostridia only slightly, and MnO_2 has no effect on either group of organisms. Under waterlogged conditions the results were quite different: the growth of *Azotobacter* is strongly stimulated by the hay, but suppressed by extra addition of MnO_2; the growth of clostridia is but slightly stimulated by the hay and not retarded by MnO_2. It would seem that MnO_2 was reduced under waterlogged conditions, and that toxic concentrations of manganese ions have inhibited the growth of *Azotobacter*, whereas on the other hand it is possible that the obligate anaerobe by adaptation has become less sensitive to such ions.

The stronger growth of *Azotobacter* in waterlogged soil agrees fully with what was found in other experiments with straw (Jensen, 1940). Two days after conclusion of the above experiment, counts were carried out from the top and bottom layers of soil with 20% moisture and 0·4% hay. Result:

	Azotobacter per gm.	Clostridia per gm.	
		Total.	Spores.
Top	100,000	5,000	4,000
Bottom	0	5,000	3,000

As might be expected, *Azotobacter* grows only on the surface of the waterlogged soil, while the clostridia seem to live in symbiosis with aerobes in the upper layers and to exist as normal anaerobes in the lower levels.

These experiments show clearly that, in the absence of an available food supply, the clostridia as well as *Azotobacter* remain largely dormant and are little influenced by the air-water relationship of the soil. In the presence of glucose or hay both groups multiply rapidly, the clostridia being especially favoured by waterlogged conditions and therefore presumably of most significance as nitrogen fixers in periods after heavy rainfalls. Being more resistant to acid reaction than *Azotobacter*, they might be of significance in this respect in many soils unsuitable for the former organism. An experiment was therefore designed to test whether the multiplication in soil is accompanied by a measurable nitrogen fixation, as a supplement to a previous series of experiments (Jensen, 1940) in which systematic counts of clostridia were not carried out, but where the conditions were usually favourable for *Azotobacter*, and where gains of nitrogen were always bound up with vigorous growth of this organism.

2. *Numbers of Clostridia and Azotobacter in Relation to Nitrogen Content of Soil.*

The soil used for this experiment was a typical wheat soil: light red loam of moderately acid reaction (pH 5·5), from Condobolin Experiment Farm, N.S.W. Before the experiment it was washed free from nitrate, air-dried, and ground very finely. The soil was used both at its original acid reaction and at a faintly alkaline reaction produced by addition of lime. Four portions of 900 gm. air-dry soil were given additions of 1·0% finely ground wheat straw, 10% of a solution containing 0·2% KH_2PO_4 and 0·005% Na_2MoO_4, and water to complete saturation (31% moisture); the water included 10 c.c. of a suspension of a soil rich in *Azotobacter* and clostridia. Two of the portions received further 0·25% $CaCO_3$. The carefully mixed portions were placed in loosely-covered glass jars where they formed a layer 15 cm. deep. The jars were incubated at 24–27°C. for 14 weeks, and samples were drawn at intervals for bacterial counts and chemical analysis. Nitrogen was determined as previously (Jensen, 1940), except that reduced iron was used instead of zinc for reduction of nitrate which, however, could hardly be detected; selenium was used as a catalyst. Organic carbon was determined by the method of Walkley and Black (1934). Owing to the high price of pyrogallic acid under the war conditions, the counts of clostridia were, after the third week, made by the dilution method in glucose solution, and are only very roughly approximate. The results are given in Table 5 (figures for carbon and nitrogen

TABLE 5.

Numbers of N-fixing bacteria and chemical changes in soil+straw.

A. Numbers of bacteria.

Inc. Days.	−$CaCO_3$			+$CaCO_3$		
	Azotobacter per gm.	Clostridia, 1,000 per gm.		*Azotobacter* per gm.	Clostridia, 1,000 per gm.	
		Total.	Spores.		Total.	Spores.
Initial	<2	0·020		<2	0·020	
7 d. *a*	(0)	6–16	16–32	11,300	3·6–8	8–32
b	(0)	6–24	8–24	1,630	6–12	1·6–3·2
14 d. *a*	1,310	6	2	6,860	4	2
21 d. *b*	60	15–20	2–4	>60,000	6–7	3–4
28 d. *a*	<15	<10		24,100	<10	
b	<15	<10		19,300	10–50	
60 d. *a*	<8	<1		39,000	>5	
b	180	<1		63,100	>5	
98 d. *a*	4	<1		30,000	>5	
b	4	<1		24,700	>5	

TABLE 5.—*Continued.*

B. Chemical changes. (Average of duplicate jars except $-CaCO_3$, 98 d.)

Series and time of incubation.	n*	Total N, p.p.m.	Gain or loss of N, p.p.m.	Organic C, %	Loss of C, %	pH.
Original	10	728±3·5		1·36		5·5
$-CaCO_3$, inc. 28 d.	8	727±3·6	−1±5·0	1·25	0·11	6·0–6·1
Do. 60 d. ..	9	727±2·6	−1±4·4	1·25	0·11	6·0
Do. 98 d. *a* ..	3	689±3·8	*−39±5·1*	1·25	0·11	6·2
b ..	5	728±5·8	0±6·8	1·23	0·13	6·2
$+CaCO_3$, 28 d. ..	8	734±1·9	+6±4·0	1·21	0·15	7·1–7·2
Do. 60 d. ..	8	724±2·9	−4±4·6	1·22	0·14	7·1
Do. 98 d. ..	7	726±4·8	−2±5·9	1·18	0·18	7·3–7·4

* Number of parallel determinations of N.

are the means of duplicate jars* which agreed completely except in one case: $-CaCO_3$, 98 days, where the separate values for each jar are given).

As was to be expected, *Azotobacter* developed vigorously in the limed soil, but only scantily in the unlimed soil which became slightly less acid during incubation. The clostridia multiplied rapidly at both reactions. The chemical data show absolutely no gain of nitrogen, even in the limed soil (the small apparent gain after 4 weeks is well below significance); it is noteworthy that *Azotobacter* is represented by numbers far lower than in previous experiments where fixation could be detected (Jensen, 1940). The only significant change is an appreciable loss of nitrogen in one jar without lime after 98 days. The loss of carbon is considerable, especially in the limed soil, and is most rapid during the first 4 weeks.

It seems clear that no considerable gains of nitrogen can be expected through the activity of clostridia in soil after heavy rains, even if, as in the present case, (*a*) nitrate is absent, (*b*) undecomposed plant residues are present, and (*c*) vigorous multiplication of the clostridia takes place, accompanied by rapid decomposition of the plant residues (in the present instance the losses of carbon during the first 4 weeks correspond to some 25–35% of all the carbon introduced with the straw).

3. *Further Observations on the Distributions of Azotobacter.*

The summer season 1938–39 was remarkable for a severe drought accompanied by an exceptional heat wave in January 1939. This afforded an opportunity of testing whether *Azotobacter* becomes particularly active after a period of dry heat (cf. Wilsdon and Ali, 1922). From the breaking of the drought (March 1939) to the early summer (November 1939) 52 soil samples were examined for the presence of *Azotobacter* by the same methods as previously (Jensen, 1940). The soils were all from the wheat belt of New South Wales, except 2 from South Australia. Another 6 samples were examined in May 1940. *Azotobacter* was found in 10 soils only, as shown below:

* The table gives the mean values and the standard error calculated according to the formula: $m = \sqrt{\frac{S(x-\bar{x})^2}{n(n-1)}}$, where $S(x-\bar{x})^2$ represents the sum of squares of deviations from the mean, and n the number of parallel determinations. Standard error of the difference: $\sqrt{m_1^2 + m_2^2}$.

Soil.	pH.	*Azotobacter.* Pellicle in mannite solution.	*Azotobacter.* Plate Count per gm.
Red loam, Forbes	5·8	+	3
Red loam, Manilla	6·0	+	21
Light brown loam, Dirnaseer	6·3	+	0
Light grey loam, Tamworth	6·3	+	1
Brown loam, Tamworth	6·6	+	1
Grey sandy loam, Cowra	6·7	+	31
Heavy brown loam, Griffith	7·7	+	0
Heavy grey loam, Narrandera	7·7	−	3
Limestone soil, Tamworth	7·7	+	48
Heavy brown loam, Griffith	8·5	+	600

Azotobacter is thus by no means more frequent than in the previous series of investigations. Most of the samples contained fresh roots of leguminous plants, especially *Medicago denticulata* and *Trifolium glomeratum*. Beijerinck (1909) referred to frequent occurrence of *Azotobacter* in the rhizosphere of legumes; this could not be corroborated from the present observations. A general survey of the distribution of *Azotobacter* in relation to soil reaction is given in Table 6, which is based on 85 data from previous observations (Jensen, 1940), the present 58, and 80 data on Victorian soils by Swaby (1939) who used a very similar method. The results depart in no way from what has been found in other parts of the world.

TABLE 6.
General Distribution of Azotobacter *in Relation to Soil Reaction.*

pH-Range.	Number of soil samples. Jensen (1940). Total.	Az.+.	Swaby (1939). Total.	Az.+.	Combined data. Total.	Az.+.	Az.+ %.
4·0–5·0	5	0	9	1	14	1	(7)
5·1–6·0	69	7	35	4	114	11	9·6±2·76
6·1–7·0	47	15	18	6	65	21	32·3±5·80
7·1–8·0	19	14	15	8	34	22	64·7±8·18
8·1–9·0	3	1	3	2	6	3	(50)
Total	143	37	80	21	223	58	26·0±2·94

Shortly after the beginning of this series of investigations there appeared a paper by Starkey and De (1939) on *Azotobacter indicum*, which is resistant to acidity, sensitive to calcium carbonate, and incapable of utilizing dextrine. Since *Az. indicum* might be of some significance in the nitrogen economy of acid soils, and since it could evidently not have been detected by the methods hitherto used, a special search was made for it in 50 of the above-mentioned soils, of pH 4·6 to 8·5, including 6 irrigated rice soils. Triplicate plate counts in a dilution 1:10 were made on agar corresponding to the saccharose solution of Starkey and De (1939), with incubation 3 weeks at 28–30°C. In no case was *Az. indicum* found, but two authentic strains (kindly supplied by Dr. R. L. Starkey, New Jersey Agr. Exp. Station, U.S.A.) grew well on the medium and produced characteristic colonies thereon when added to soil suspension. The method is thus adequate, and it seems that *Az. indicum* does not occur at all in Australian soils, or else it must be so rare as to be without any practical significance.

Several plates of saccharose-agar showed big slimy colonies of a polysaccharide-forming yeast; 3 strains of this and 6 strains of bacteria of the type studied by Selim (1931) were tested for nitrogen-fixing power. The bacteria were isolated from wheat

soils by inoculation into soil extract with glucose, and plating on corresponding agar; two of them were similar to the "bacille gommeux" of Winogradsky (1926), one apparently identical with *Bac. malabarensis* Löhnis and Pillai (1907), and 3 were gas-producing rods of the *Bact. aerogenes*-type. Tests for nitrogen fixation were done by cultivation for 20 to 30 days at 28–30°C. in (*a*) Starkey and De's saccharose agar, (*b*) corresponding solution with 2% soil (cf. Selim, 1931), and (*c*) NO_3-free soil extract with 2% glucose and mineral nutrients including molybdenum. *Azotobacter* and *Rhizobium trifolii* were grown as controls. Neither the tested organisms nor the rhizobia showed nitrogen fixation; the change in N-content of cultures before and after incubation never exceeded 0·13 mgm. under conditions where *Azotobacter* fixed from 1 to 7·2 mgm. N per culture, or up to 14 mgm. per gm. of sugar supplied. In view of these and previous results (Jensen, 1940) we may safely conclude that no further attention need be given to the possibility of gains of nitrogen in soil through the agency of non-symbiotic microorganisms other than *Azotobacter*, clostridia, and blue-green algae.

Summary.

Waterlogged soil conditions and presence of decomposible organic matter (glucose or oaten hay) were found to promote the development of *Clostridium butyricum*, which also occurred in fairly large numbers in aerated soil, presumably by existing in association with aerobes. In the absence of glucose or hay, clostridia as well as *Azotobacter* remained largely dormant without being much influenced by the air-water relationship of the soil. Manganese dioxide depressed the numbers of *Azotobacter* in saturated soil with hay, but had no effect on the clostridia, or on *Azotobacter* in aerated soil.

Nitrogen fixation could not be detected in acid or neutral, water-saturated soil incubated with addition of wheat straw, in spite of good multiplication of the clostridia at both reactions, and vigorous decomposition of the organic matter of the straw. No appreciable gains of nitrogen in the soil through the activity of clostridia can therefore be expected in periods during and after heavy rains.

No evidence was found that *Azotobacter* is prominent in soil after droughts, or in the rhizosphere of leguminous plants. The acid-resistant *Az. indicum* was not found in Australian soils, nor any other aerobic organism capable of non-symbiotic nitrogen fixation.

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THE SEX-RATIO IN THE WILD ANIMAL POPULATIONS OF THE NEW HEBRIDES.

By A. J. Marshall and John R. Baker, D.Sc.

[Read 27th November, 1940.]

The chief biological object of the Oxford University Expedition to the New Hebrides (1933–4) was the study of the breeding seasons of animals in a remarkably unvarying climate, but we kept a careful record of all specimens obtained with a view to reporting on the sex-ratio. Our collections were made chiefly in eastern Espiritu Santo, though specimens were also taken in the west and in the small island of Gaua. We soon noticed that the great majority of our vertebrates showed a remarkable preponderance of males. The same peculiarity is shown by the natives of the islands, and those of the district called Sakau have one of the highest sex-ratios of any people in the world (see Baker, 1928).*

In this paper we report on the birds and mammals. The sex-ratio is given as the percentage of males, and the standard error of the ratio has been calculated from the formula $\sqrt{\frac{mf}{n}}$, where m is the percentage of males, f that of females, and n the total number of specimens counted.

The birds will be considered first.

All species of which we shot 40 or more specimens are considered in what follows. There are 20 such species and the total number of individuals shot of these species (of all ages) was 2,193. The sex-ratio of the whole group was 59 ± 1·0. Of the 20 species, only 3 had an excess of females, and in no case was such excess of females statistically significant. The highest sex-ratios were as follow:

Cacomantis pyrrophanus (cuckoo)	84 ± 4·9
Myzomela cardinalis (honey-eater)	81 ± 3·6
Rhipidura brenchleyi (flycatcher)	68 ± 5·8
Halcyon chloris (kingfisher)	67 ± 6·5
Turdus poliocephalus (blackbird)	65 ± 6·7

Of the total of 2,193 birds, 319 were juvenile. It is interesting to notice that the sex-ratio of the juveniles was as high (60 ± 2·7) as that of the adults (58 ± 1·1). We did not obtain any young *Cacomantis*, but in *Myzomela cardinalis* the sex-ratio of young was 78 ± 5·9 and of adults 83 ± 4·5. These figures show that high sex-ratio is not to any significant extent a product of differential mortality of the sexes in the later stages of growth.

The fact that sex-ratio is as high in young as in adults also shows that the preponderance of males is not due simply to the females being too much occupied with incubation to be shot. Other lines of evidence point in the same direction. Thus the highest sex-ratio of all (84 ± 4·9) is in a cuckoo, which does not incubate at all; and the flycatcher and kingfisher have high ratios, though in these families it is usual for both sexes to incubate. We do not think that our shooting was selective. Natives were nearly always paid the same price for specimens of each sex: when we were paying more for one sex, we neglected the birds received in our studies of sex-ratio. On the whole males have brighter plumage, but there is no direct correlation here with sex-ratio. Thus the male *Myzomela* is brilliantly-coloured and the female dull, and the species has a ratio of 81; but in *Cacomantis*, *Rhipidura brenchleyi*, and *Halcyon*,

* We particularly wish to acknowledge our indebtedness to T. H. Harrison.

which also have very high sex-ratios, the sexes hardly differ externally. Further, in most of the species under consideration both sexes attend the nest and young. We do not think that bright plumage makes birds much easier to see, particularly under rain-forest conditions. A significant observation is that the young males of *Myzomela* are indistinguishable to the shooter from females, yet the sex-ratio of the young is just as high as that of the adults.

There appears to be some tendency for related birds to have similar sex-ratios. Thus two of the three birds which showed an excess of females were Campophagidae (both 49). The pigeons do not have very high ratios (59, 54, 53, 44). All three flycatchers have high ratios (68, 64, 62).

When the sex-ratio is very high, there must be much competition for hens. Most of the adult males of *Myzomela* have bare patches on their scarlet heads, presumably caused by fighting. This might suggest that a high ratio was of some benefit to the species, since the more virile males would breed and so a hardier stock might result. At the same time this does not mean that the sex-ratio is adaptive.

In addition to the shot birds reported upon above, we obtained and sexed 73 nestlings of the 20 species. It is unfortunate that the number was too small for a statistical study, but it is suggestive that 36 were males and 37 females. One is encouraged to think that the high sex-ratio of shot birds is caused by a greater mortality of females in the early days after leaving the nest.

Among the few mammals present in the islands we only collected enough specimens of two species for study of sex-ratio. These were the insectivorous bat, *Miniopteris australis*, and the large fruit-bat, *Pteropus geddiei*.

Miniopterus was collected by beating the air with sticks in the large cave in which it abounds. Only fully-grown specimens were obtained. It has a sharply-defined breeding season, during which the sex-ratio was found to be 66 $\pm$ 3·0; but it is clear that at this season the females avoid being killed, for in the long non-breeding season the ratio is 51 $\pm$ 1·9. We have here a species with approximate equality of the sexes.

In the fruit-bat the females retire to the depths of the forest when pregnant and are very difficult to obtain. It would be useless to try to estimate the sex-ratio at this time of the year. In the non-breeding season the females live socially with the males. We obtained specimens by shooting, and there is no question of differential shooting, for one cannot determine the sex until the animal has been shot. The sex-ratio, in the non-breeding season, is 69 $\pm$ 3·3. This includes some young ones, too few for separate statistical consideration.

It is difficult to believe that the high sex-ratio of New Hebridean animals could be adaptive, and indeed it seems probable that sex-ratio is seldom adaptive, except in those special cases in which male-producing sperms are eliminated in the testes (as in Aphids) or in which sex determination depends on whether the egg is or is not fertilized (as in aculeate Hymenoptera).

In most wild animals it appears that the sex-ratio is a matter of chance, with a tendency for the primary ratio to be near 50. It seems that in most mammals the male-producing sperms have some advantage in achieving fertilization (Crew, 1937), but there is no evidence that this is adaptive. Again, there is often differential death of the sexes, but here again there is no evidence that the primary sex-ratio is adapted to result in a ratio of value to the species. Differential mortality in a wild animal was strikingly demonstrated by Sasaki (1926). He found the sex-ratio of wild goldfish in Japan, lumping all specimens together, to be extraordinarily low, namely 11. Small specimens, 3–4 cm. long, showed a much higher ratio (32). There is clearly selective elimination of males during growth. Geiser (1924) has reported on the preponderance of females in the top-minnow, *Gambusia*, and has shown that there is nothing in spermatogenesis to account for it. As a rule the sex-ratio in marine Teleosts approaches equality, as Craigie (1927) has shown: this presumably indicates absence of differential mortality. In Elasmobranchs there is a tendency towards excess of females. In wild birds it is not rare to find an excess of males: thus Friedmann (1927) reports a sex-ratio of about 60 in three species of cow-bird (*Molothrus* and *Tangavius*).

It may be suggested that the ordinary chromosome mechanism of sex determination presents such advantages of simplicity as to outweigh any advantages which might accrue from adaptation of sex-ratio to the needs of the species. In those animals in which the male does not incubate eggs or protect female or young or territory, he is useless to the species except as a sort of dice-box for producing new combinations of genes in his sperms. It is difficult to believe that this function requires so many males as occur in most non-parthenogenetic species. Perhaps the Lamellibranch, *Teredo*, has adapted its sex-ratio to its requirements by somehow reducing the percentage of males to 0·2 (Pelseneer, 1906).

Summary.

There is a preponderance of males in the birds of the New Hebrides. It is argued that the sex-ratio is in general non-adaptive.

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AVES.

	Total No. shot.	Sex-ratio.
Columbae.		
Ptilinopus greyi	92	53 ± 5·2
Pt. tannensis	46	59 ± 7·2
Macropygia rufa	50	44 ± 7·0
Chalcophaps chrysochlora	81	54 ± 5·5
Coccyges.		
Cacomantis pyrrophanus	55	84 ± 4·9
Psittaci.		
Trichoglossus ornatus	419*	55 ± 2·4
Halcyones.		
Halcyon chloris	52	67 ± 6·5
Passeres.		
Rhipidura brenchleyi	65	68 ± 5·8
R. spilodera	69	62 ± 5·8
Passeres (contd.).		
Myiagra caledonica	42	64 ± 7·4
Coracina caledonica	80	49 ± 5·6
Neolalage banksiana	74	49 ± 5·8
Turdus poliocephalus	51	65 ± 6·7
Artamus leucorhynchus	54	54 ± 6·8
Pachycephala pectoralis	396	60 ± 2·5
Clytorhynchus pachycephaloides	99	56 ± 5·0
Zosterops lateralis	153	57 ± 4·0
Z. flavifrons	112	54 ± 4·7
Myzomela cardinalis	120	81 ± 3·6
Aplonis zeylanica	83	51 ± 5·5
All the above species together	2193	59 ± 1·0

MAMMALIA.

Cheiroptera.		
Miniopterus australis†‡	716	51 ± 1·9
Pteropus geddiei†	201	69 ± 3·3

* 48 specimens of unstated age not included.

† In non-breeding season.

‡ Killed with sticks.

AUSTRALIAN HESPERIIDAE. IX.

DESCRIPTION OF A NEW SPECIES.

By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

[Read 27th November, 1940.]

Anisynta albovenata, n. sp.

♂. Upperside grey-brown, with cilia paler. Forewing with six white spots, one distinct near end of cell; two small, subapical, upper faint; two faint below these in 4 and 5 and another in 2. Hindwing unmarked.

Underside grey-brown. Forewing, spots as above but smaller and yellowish, subapicals very faint; veins towards termen lined with white. Hindwing with veins lined with white, including the folds representing vein 5 and the internal veinlet in cell; very faint trace of a discal series of whitish spots.

♀. Upperside grey-brown, with cilia paler. Forewing with nine white spots, one large near end of cell; three subapicals; two below these nearer termen in 4 and 5; two larger further from termen in 2 and 3 and a smaller spot above vein 1. Hindwing unmarked.

Underside grey-brown. Spots as above but smaller and, except subapicals, yellowish; veins in outer area of forewing and on hindwing white as in male; discal band of spots of hindwing in some specimens more defined.

Antennae strongly ringed with white. Forewing narrow, apex acute.

The species is a typical *Anisynta* and allied to *A. cynone gracilis* Tepper 1882, but larger. The very distinctive underside at once distinguishes it from all other Australian Hesperiids. It is a spring species, while *A. cynone* has only been taken in the autumn.

I have before me six specimens all caught on 13th Oct., 1940, by Mr. M. W. Mules near the sea coast on Point Pierce, Yorke's Peninsula, South Australia. The holotype will be placed in the Australian Museum, Sydney, and two of the series returned, appropriately labelled, to Mr. Mules, who is to be congratulated on his success in finding such a distinctive new species.

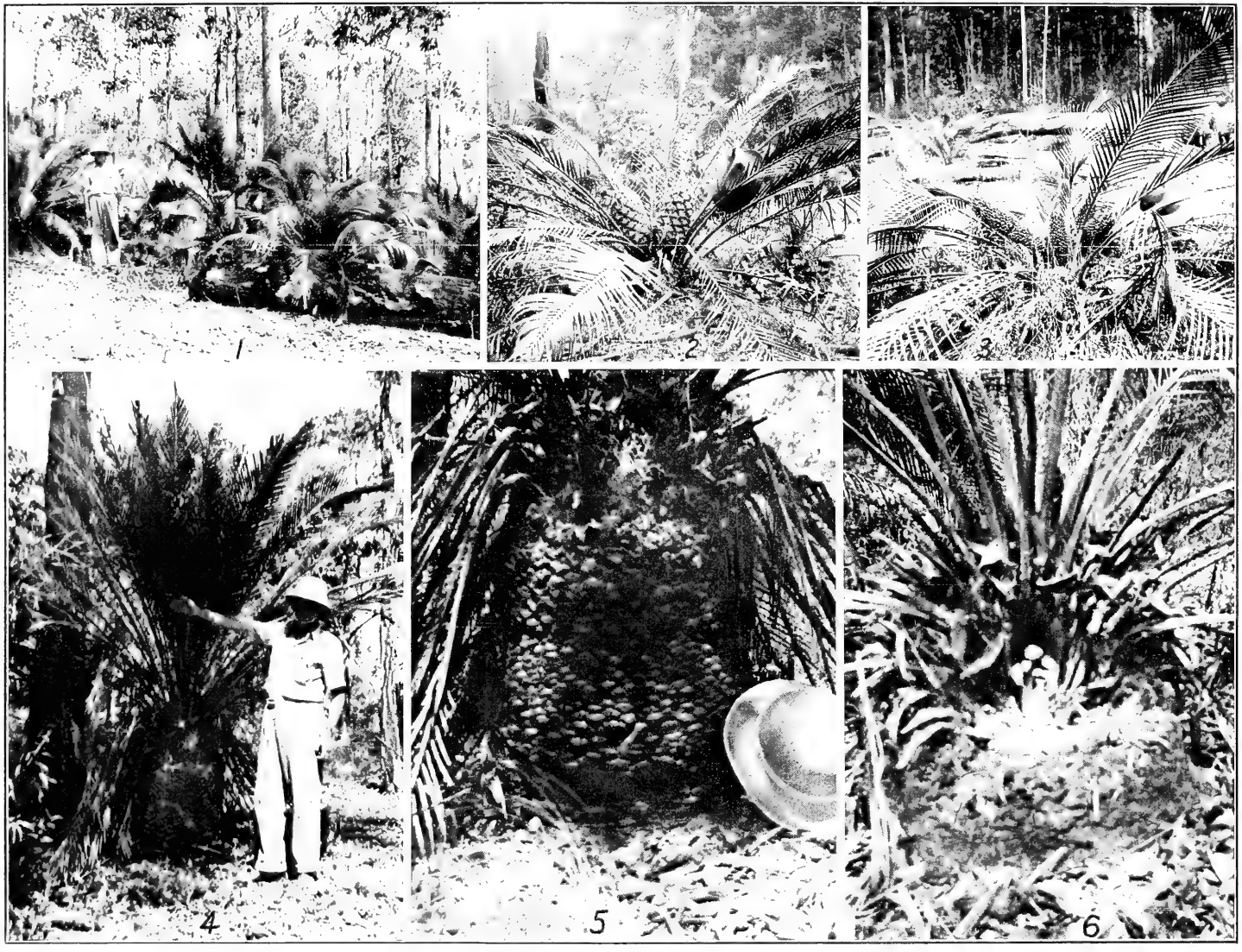
Anisynta cynone Hewitson, 1874.

Mr. F. M. Angel has sent me further specimens from South Australia and I am now able to assign a locality for the holotype male in the British Museum.

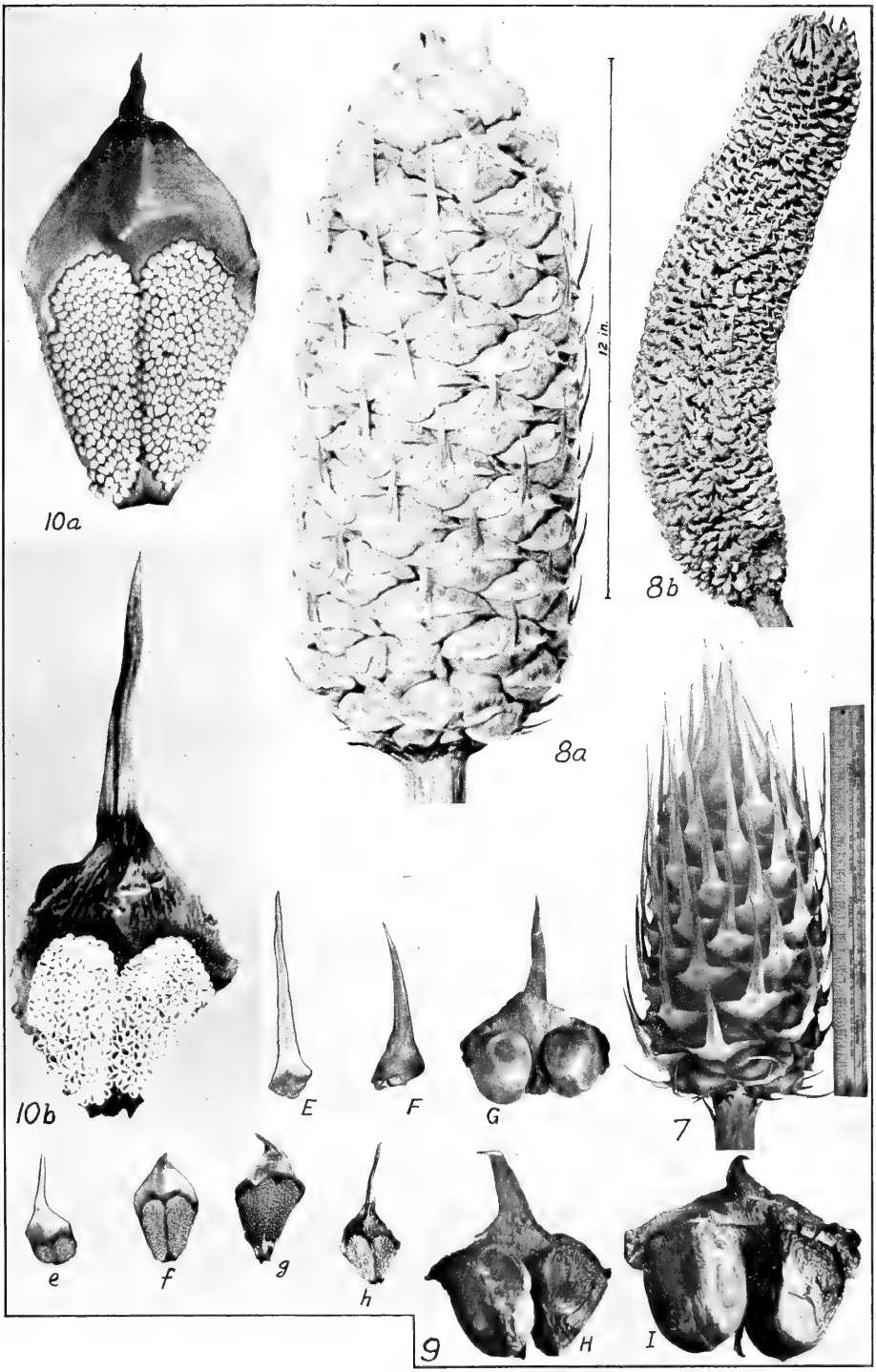
I find that all specimens seen from Goolwa, Port Elliot and Robe are rufous brown with yellowish spots above. The underside is variable, but I have two specimens from Robe which are very close to an excellent coloured drawing of the holotype made for me in London. I therefore assign the type locality as the mouth of the Murray River and suggest the holotype was caught by Frederick Strange on Sturt's Expedition.

The race *gracilis* Tepper 1882 from further north is grey-brown with white spots and is typically from Salisbury. I place here specimens from Henley Beach, Largs Bay, Rosewater and Burra.

The race *grisea* Waterhouse, 1932, is from Kerang, Victoria, on the Murray River.

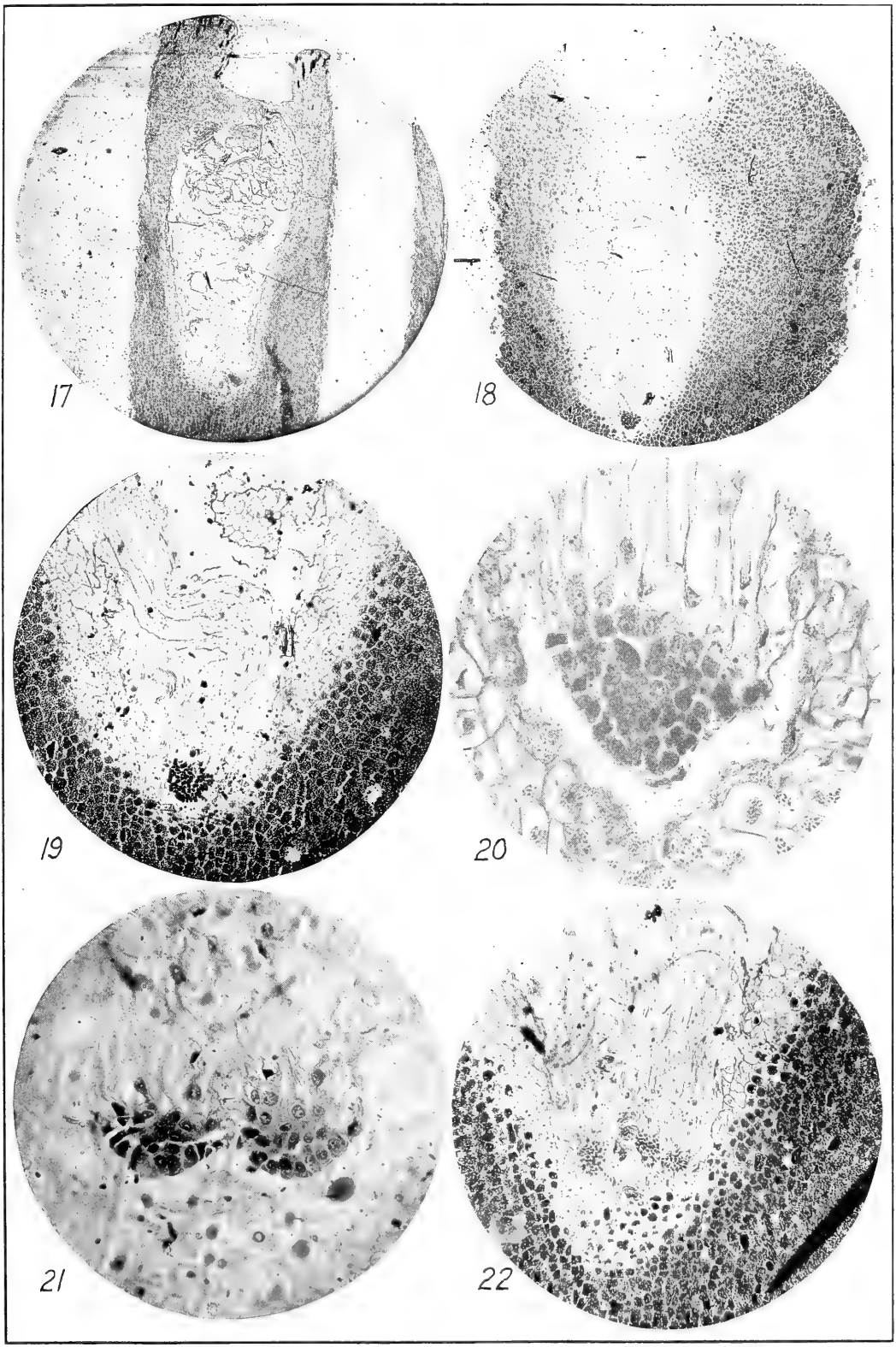


Macrozamia spiralis.



Macrozamia spiralis.

Macrozamia spiralis.



Macrozamia spiralis.

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

27th March, 1940.

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

The Donations and Exchanges received since the previous Monthly Meeting (29th November, 1939), amounting to 32 Volumes, 387 Parts or Numbers, 22 Bulletins, 16 Reports and 23 Pamphlets, received from 141 Societies and Institutions and 3 private donors, were laid upon the table.

PAPERS READ.

1. Contributions to the Nitrogen Economy of Australian Wheat Soils with particular Reference to New South Wales. By H. L. Jensen, Macleay Bacteriologist to the Society.

2. Studies in Australian Embioptera. iv. Supplementary Taxonomic Notes. By Consett Davis, M.Sc.

3. Taxonomic Notes on the Order Embioptera. xv. By Consett Davis, M.Sc.

4. Notes on the Life-history of *Limnophora nigriorbitalis* Malloch (Diptera, Anthomyiidae). By Kathleen M. I. English, B.Sc.

5. The Upper Palaeozoic Rocks in the Country between the Manning and Karuah Rivers, N.S.W. By A. H. Voisey, M.Sc.

ORDINARY MONTHLY MEETING.

24th April, 1940.

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

Miss Joan M. Crockford, Gladesville, Dr. K. H. L. Key, Hunter's Hill, Miss Marjorie L. B. Proctor, Killara, and Mrs. M. H. B. Robertson, Petersham, were elected Ordinary Members of the Society.

The President referred to the sudden death on 16th April, 1940, of Mr. H. J. Carter, who had been a member of the Society since 1903, a Member of Council from 1920 to 1939, and President, 1925–26. Mr. Carter was very widely known for his work on several families of the Coleoptera.

The Donations and Exchanges received since the previous Monthly Meeting (27th March, 1940), amounting to 16 Volumes, 173 Parts or Numbers, 8 Bulletins, 2 Reports and 2 Pamphlets, received from 67 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Studies in Applied Ecology. i. A Statistical Analysis of Regeneration following Protection from Grazing. By Ilma M. Pidgeon, M.Sc., Linnean Macleay Fellow of the Society in Botany, and Professor Eric Ashby.

2. On the Interpretation of certain Features of the Embryonic Skull of Platypus. By H. Leighton Kesteven, D.Sc., M.D.

3. A Permian Blastoid from Belford, N.S.W. By Joan M. Crockford and Ida A. Brown, D.Sc.

NOTES AND EXHIBITS.

Mr. E. Cheel exhibited specimens of the Ergot of Pharmacy (the winter resting stage of *Claviceps purpurea*) obtained from a wholesale druggist in Sydney.

As this is a serious fungus disease of grain-crops, which causes foot-rot and abortion in sheep and cattle, it is prohibited from being imported in accordance with the Quarantine (Plants) Regulations which require a statutory declaration from all wholesale druggists that it is to be used for medicinal purposes only. It is recorded in various text-books on Agriculture and in scientific journals that this fungus disease is parasitic on wheat, barley, oats, rye-crops, rye-grass, false-brome, awnless-brome, canary grass, Texas grass, sugar-cane, sugar-grass, tall, oat-grass, and Australian blue-grasses. In view of the above, it appears to be more preferable to use Cotarninae Hydro-chloridium, known in the trade as Stypyicin, for medical treatment than Ergot.

Dr. H. L. Jensen exhibited cultures of cellulose-decomposing bacteria on filter paper impregnated with manganese dioxide, showing formation of oxy-acids (by dissolution of the MnO_2) by organisms capable of providing nitrogen-fixing bacteria with food material from the cellulose.

Miss Valerie May exhibited a specimen of *Loranthus pendulus* Sieb. from Kendall, N.S.W. The exhibit differed from the normal of the species in that in some cases four flowers were associated in the partial cymes instead of the normal three.

The Secretary communicated a note from the Rev. H. M. R. Rupp concerning a revised determination of the specimens referred to *Cheirostylis grandiflora* Blume by the late Mr. J. H. Maiden in the Society's Proceedings (1896, p. 625). A note on this determination is to appear in the next issue of "*Contributions from the National Herbarium*".

ORDINARY MONTHLY MEETING.

29th May, 1940.

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

The President announced that the Council had elected Mr. C. A. Sussmilch, Mr. E. C. Andrews, Mr. T. C. Roughley and Professor J. Macdonald Holmes to be Vice-Presidents for the Session 1940–41.

The President also announced that the Council had elected Dr. G. A. Waterhouse to be Honorary Treasurer for the Session 1940–41.

The Donations and Exchanges received since the previous Monthly Meeting (24th April, 1940), amounting to 6 Volumes, 66 Parts or Numbers, 2 Bulletins, 2 Reports and 1 Pamphlet, received from 47 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. The Food Plants or Hosts of some Fijian Insects. iv. By W. Greenwood, F.R.E.S. (*Communicated by Dr. A. B. Walkom.*)

2. The Ecology of the Central Coastal Area of New South Wales. iii. Types of Primary Succession. By Ilma M. Pidgeon, M.Sc., Linnean Macleay Fellow of the Society in Botany.

3. The Geomorphology of the Hunter River District, N.S.W. By C. A. Sussmilch, F.G.S.

NOTES AND EXHIBITS.

Miss Valerie May exhibited seven species of algae, believed to be new records for New South Wales. These are: Chlorophyceae: *Caulerpa racemosa* J. Ag. var. *laetevirens* f. *typica* Weber van Bosse, Coll. Angourie, Jan., 1936, Dr. L. Fraser; *Caulerpa racemosa* J. Ag. sub-species *C. peltata* Lamour., var. *nummularia* Weber van Bosse, Coll. Angourie, Jan., 1936, Dr. L. Fraser; also Woolgoolga, June, 1937, Valerie May; *Halimeda Tuna* (Ell. et Soland.) Lamour., Coll. Angourie, Jan., 1936, Dr. L. Fraser; *Valonia confervoides* Harv., Coll. Angourie, Jan., 1936, Dr. L. Fraser (no species of *Halimeda* or *Valonia* has been recorded from New South Wales previously); Rhodophyceae (identified by Prof. W. Troll, Germany): *Bostrychia*

flagellifera Post., Coll. George's River, July, 1938, Valerie May, on roots of *Avicennia* and *Aegiceras*; *Bostrychia Moritziana* Ag., Coll. George's River, July, 1938, Valerie May, on roots of *Avicennia* and *Aegiceras*; *Catenella Nipae* Zanard., Coll. George's River, July, 1938, Valerie May, on roots of *Avicennia* and *Aegiceras*. These Rhodophyceae are fairly plentiful in the mangrove swamps of the Sydney district and, with others, appear to be important ecologically.

Mr. E. Cheel exhibited a portion of a shrub about five feet long taken from a plant of *Callistemon linearis* cultivated at Ashfield, showing the delayed dehiscence characteristic of several species of the genus *Callistemon*. The specimen displayed a series of spiked capsules in different stages of development which resulted from flowers produced in October, 1936, 1937, 1938 and 1939. When cut from the parent plant in January 1940, the valves of the capsules resulting from flowers produced in 1936 and 1937 shed their seeds freely and have germinated successfully. The valves of the capsules from the flowers of 1938 and 1939 are unopened, which clearly shows that they are not sufficiently matured to shed their seeds. He also exhibited seedling plants of "Blueberry Ash" (*Elaeocarpus reticulatus*) with "shoot-bearing tumorous growths", somewhat similar to those commonly produced on *Eucalyptus* and *Angophora* seedlings (see These PROCEEDINGS, xliii, 1918, p. 191, for further particulars concerning the latter).

ORDINARY MONTHLY MEETING.

26th JUNE, 1940.

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

Miss E. M. Basnett, B.Sc., Epping, and Mr. K. L. Taylor, Sydney, were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (29th May, 1940), amounting to 4 Volumes, 125 Parts or Numbers, 2 Bulletins, 7 Reports, 3 Pamphlets and 1 Map, received from 70 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Notes on Australian Diptera. No. xxxviii. Chloropidae. Part ii. By J. R. Malloch. (*Communicated by F. H. Taylor, F.R.E.S., F.Z.S.*)

2. On the External Morphology and Biology of *Heteronychus sanctae-helenae* Blanch., and *Metanastes vulgivagus* Olliff (Coleoptera, Scarabaeidae). By D. Margaret Cumpston, M.Sc., Linnean Macleay Fellow of the Society in Zoology.

3. An Empusa on a Mite. By T. Petch. (*Communicated by Dr. A. J. Nicholson, F.R.E.S.*)

4. Tabulation of the Genera *Austrolimnius* and *Notriolus* (Dryopidae) and Description of a New Species of *Nyctozoilus* (Tenebrionidae). By the late H. J. Carter, B.A., F.R.E.S.

NOTES AND EXHIBITS.

Miss Valerie May exhibited a green alga, which was collected as free-floating material in the surf at Byron Bay, N.S.W., on 16th January, 1940. The plant was reported as very plentiful in that district at the time, and was causing many complaints from the local fishermen. The identification (kindly checked by Royal Botanic Gardens, Kew) is *Enteromorpha plumosa* Kuetz. (= *E. Hopkirkii* M'Calla). This is a new record for New South Wales.

ORDINARY MONTHLY MEETING.

31st JULY, 1940.

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

Dr. A. A. Abbie and Mr. Gordon Pasfield were elected Ordinary Members of the Society.

The President announced that the proclamation protecting certain wildflowers and native plants had been renewed for a further period of one year from 1st July, 1940, *Casuarina Cunninghamiana* (River Oak) having been added to the list of protected plants this year.

The President, on behalf of members, expressed congratulations to Dr. H. G. Raggatt on his appointment as Assistant Geological Adviser to the Commonwealth Government.

The Donations and Exchanges received since the previous Monthly Meeting (26th June, 1940), amounting to 9 Volumes, 105 Parts or Numbers, 11 Bulletins, 2 Reports and 5 Pamphlets, received from 59 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Taxonomic Notes on the Order Embioptera. xvi–xvii. By Consett Davis, M.Sc.

2. Further Observations on the Trombidiid Larvae of New Guinea (Acarina: Trombidiidae). By C. E. M. Gunther, M.B., B.S., D.T.M.

3. A Listrophorid Parasite of the Wallaby from New Guinea. By C. E. M. Gunther, M.B., B.S., D.T.M.

4. The Musculature of the Mandibular and Hyoid Arches in a Sting-Ray (*Trigonorhina fasciata*). By G. S. Lightoller, M.D. (*Communicated by Professor A. N. Burkitt.*)

ORDINARY MONTHLY MEETING.

28th August, 1940.

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

The Donations and Exchanges received since the previous Monthly Meeting (31st July, 1940), amounting to 12 Volumes, 104 Parts or Numbers, 6 Bulletins, 2 Reports and 1 Pamphlet, received from 56 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. Taxonomic Notes on the Order Embioptera. xviii. By Consett Davis, M.Sc.

2. The Silurian Rugosa of the Yass-Bowning District, N.S.W. By Dorothy Hill, M.Sc., Ph.D.

ORDINARY MONTHLY MEETING.

25th September, 1940.

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

Messrs. F. L. Milthorpe, B.Sc.Agr., and J. M. Vincent, B.Sc.Agr., were elected Ordinary Members of the Society.

The President announced that the Council is prepared to receive applications for four Linnean Macleay Fellowships tenable for one year from 1st March, 1941, from qualified candidates. Applications should be lodged with the Secretary, who will afford all necessary information to intending candidates, not later than Wednesday, 6th November, 1940.

The Donations and Exchanges received since the previous Monthly Meeting (28th August, 1940), amounting to 4 Volumes, 54 Parts or Numbers, 8 Bulletins and 4 Pamphlets, received from 33 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Revision of Australian Lepidoptera. Oecophoridae. ix. By A. Jefferis Turner, M.D., F.R.E.S.

2. Four Larval Trombidiidae from British North Borneo (Acarina: Trombidiidae). By C. E. M. Gunther, M.B., B.S., D.T.M.

3. Notes on the Synonyms of *Trombicula minor* Berlese 1940. By C. E. M. Gunther, M.B., B.S., D.T.M.

4. The Osteogenesis of the Base of the Saurian Cranium and a Search for the Parasphenoid Bone. By H. L. Kesteven, D.Sc., M.D.

NOTES AND EXHIBITS.

Miss A. Melvaine exhibited specimens of *Verbena litoralis* H.B. & K. from Sirius Cove, Mosman. This species does not appear to have been recorded previously from New South Wales. It is a native of tropical America.

Mr. E. Cheel exhibited live plants of *Boronia safrolifera* in full flower, cultivated from plants collected at Broadwater, Richmond River district, in October, 1939. Live plants of *Boronia floribunda* and *Boronia pinnata* were also exhibited for comparison. Flowering plants of three distinct species of "Australian Bluebells" (*Wahlenbergia*) were exhibited, two of which were grown from seed collected in the Tamworth district and breed true to type, and are quite distinct from the common form of the Port Jackson district. Bentham's description of *W. gracilis* is a composite one and includes nine species, the types of which should be closely examined before a clear definition can be given as to the correct nomenclature for the different forms. An interesting series of specimens of *Callistemon*, including *C. roseus*, *C. paludosus* and *C. viminalis*, with capsules and seeds fully matured from last year's flowers were exhibited to illustrate two well-defined sections of the genus. The section Eucallistemon requires two or more years to produce fully developed capsules and reddish-brown linear seeds. The section Tubulosa, which includes *C. viminalis* with the filaments cohering into a well-defined tube at the base, has the capsules and wedge-shaped straw-coloured seeds fully matured in ten to twelve months after the flowering period. The capsules and seeds of *C. roseus* and *C. paludosus* are very similar to those of *C. viminalis* but the filaments are quite free. A flowering branch of the "Native Wistaria" (*Millettia*) cultivated at Ashfield was also shown.

ORDINARY MONTHLY MEETING.

30th October, 1940.

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

The President announced that the Council has accepted the resignation of Dr. A. B. Walkom as Secretary of the Society in consequence of his appointment as Director of the Australian Museum, the resignation to take effect as from 31st October, 1940; also that the Council has elected Dr. Walkom as Honorary Secretary of the Society from 1st November to 31st December, 1940.

The President also announced that the Council has accepted the resignation of Mr. R. J. Swaby, Biochemist, as Assistant to the Macleay Bacteriologist. Applications for appointment as temporary assistant to the Bacteriologist have been invited by advertisement in the *Sydney Morning Herald* of 19th October, and close on 4th November, 1940.

The President reminded candidates for Linnean Macleay Fellowships, 1941–42, that Wednesday, 6th November, 1940, is the last day for receiving applications.

The Donations and Exchanges received since the previous Monthly Meeting (25th September, 1940), amounting to 12 Volumes, 66 Parts or Numbers, 2 Bulletins and 2 Pamphlets, received from 46 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. New and Known Nematodes from Australian Marsupials. By Prof. T. Harvey Johnston, M.A., D.Sc., F.L.S., and Patricia M. Mawson.

2. An Investigation of the Life-cycle of *Macrozamia spiralis* Miq. By P. Brough, M.A., D.Sc., F.R.S.E., and Marjorie H. Taylor, B.Sc.

3. Miscellaneous Notes on Australian Diptera. vii. On Body-colour and on Species of Tabanidae, Cystidae, and Asiloidea. By G. H. Hardy.

NOTES AND EXHIBITS.

Mr. E. Cheel exhibited (1) a seedling *Callistemon* raised from *C. hortensis*, showing a distinctly lilac-rose, or lilac-carmine colour instead of garnet as in the parent plant, (ii) a series of fresh flowering specimens from cultivated plants of the following species: *C. pinifolius*, *C. linearis* and *C. acuminatus*, (iii) specimens of *Diploglottis Campbelli* taken from a cultivated plant together with a seedling plant raised from last year's flowers.

Mr. R. T. Baker exhibited a fungus which had grown through a tar-paved road.

Mr. J. A. Dulhunty exhibited apparatus devised for examination of the effects of infra-red radiation on sections of torbanite of standard thickness.

Dr. A. B. Walkom drew attention to three reports on the excursions to the Western Districts of New South Wales made in September, 1939. The reports are by Miss C. D. J. Back, Miss L. M. Cameron and Mr. N. C. Beadle. They will be deposited in the library of the University of Sydney where they will be available for reference.

ORDINARY MONTHLY MEETING.

27th November, 1940.

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

Messrs. P. C. W. Shaw, M.Inst.C.E., and W. L. Wearne were elected Ordinary Members of the Society.

The President referred to the death of Mr. William Mountier Bale, F.R.M.S., on 4th October, 1940, aged 89. Mr. Bale had been a Corresponding Member of the Society since 1888.

The President announced that the Council had selected Dr. N. S. Noble for appointment as Secretary of the Society as from 2nd January, 1941.

The President also announced that the Council had reappointed Miss Ilma M. Pidgeon, M.Sc., and Mr. J. A. Dulhunty, B.Sc., to Linnean Macleay Fellowships in Botany and Geology respectively, for one year from 1st March, 1941, and had appointed Mr. Mervyn E. Griffiths, M.Sc., and Dr. Germaine A. Joplin, B.Sc., to Linnean Macleay Fellowships in Physiology and Geology respectively, for one year from 1st March, 1941.

The Donations and Exchanges received since the previous Monthly Meeting (30th October, 1940), amounting to 4 volumes, 65 Parts or Numbers, 2 Bulletins, 1 Report and 2 Pamphlets, received from 45 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. Taxonomic Notes on the Order Embioptera. xix–xx. By Consett Davis, M.Sc.

2. Nitrogen Fixation and Cellulose Decomposition by Soil Microorganisms. i. Aerobic Cellulose-Decomposers in association with *Azotobacter*. By H. L. Jensen, Macleay Bacteriologist to the Society.

3. The Sex-ratio in the Wild Animal Populations of the New Hebrides. By A. J. Marshall and John R. Baker, D.Sc.

4. Further Investigations on the Nitrogen-fixing Bacteria in Soil. By H. L. Jensen and R. J. Swaby, B.Sc.Agr.

5. Australian Hesperiidae. ix. Description of a New Species. By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.

NOTES AND EXHIBITS.

Dr. G. A. Waterhouse exhibited the new butterfly described in his paper and pointed out that further discoveries might be made in the coastal region and the islands of the Great Australian Bight.

GENERAL INDEX.

(1940.)

LIST OF PLATES.

PROCEEDINGS, 1940.

LIST OF GENERA AND SPECIES DESCRIBED AS NEW IN THIS VOLUME (1940).

Genera.

Species.

CORRIGENDA.

Proceedings, 1940.

Page xx, line 12, *for* Algebunga, *read* Alberga

Page 48, line 9 below, *for* x, *read* $\bar{x}$

Page 101, heading of Table 27: *for* 19/6/37, *read* 29/6/37

Page 113, line 12, *for* and (last word) *read* sand

Page 117, line 6, *for* Pflanzenwachetums, *read* Pflanzenwachstums

Page 121, line 20, *for* Vorarbeitung *read* Verarbeitung

Page 183, line 13 from bottom, *for* specimen *read* species

Page 190, Key, second line of dichotomy 3, *for* smaller, less than ten, *read* smaller, more than ten

Page 327, line 24, *for* synonyms *read* synonymous

Page 384, line 6 from bottom, *for* subspecies *read* species

Page 421, line 24 and where mentioned, for *Machaeretis* read *Machaeritis*

Proceedings, 1939.

Pages 567–572, for *Berlandiella* read *Berlandembia*

Pages 573–575, for *Saussurella* read *Saussurembia*

For notes on these two changes see Proceedings, 1940, p. 191.

Note.—In this Volume the list of donations and exchanges, the list of members, and the Biological Index have been omitted as a result of rationing of paper supplies.

(Issued 15th May, 1940.)

Vol. LXV.
Parts 1-2.

Nos. 287-288.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1940.

Parts I–II (Pages i–xviii; 1–210).

CONTAINING THE PROCEEDINGS OF THE ANNUAL MEETING AND PAPERS READ IN MARCH-APRIL.

With five plates.
[Plates i-v.]

SYDNEY:
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1940.

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The Linnean Society of New South Wales

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(To be elected at Council Meeting, 22nd May, 1940.)

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G. A. Waterhouse, D.Sc., B.E.
W. L. Waterhouse, D.Sc.Agr.
A. R. Woodhill, B.Sc.Agr.

Auditor: F. H. Rayment, F.C.A.(Aust.).

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With the exception of Volume II, Part 4, Volume V, Part 2, and Volume VI, Part 4, of the First Series, the Publications of the Linnean Society of New South Wales may be obtained from the Society, Science House, 159 Gloucester Street, Sydney, or from David Nutt, 212 Shaftesbury Avenue, London, W.C.2. The stock of copies of First Series, Volumes I to VI (1875–1881), is limited.

Year.	Part 1.	Part 2.	Part 3.	Part 4.	Year.	Part 1.	Part 2.	Part 3.	Part 4.
	s. d.	s. d.	s. d.	s. d.		s. d.	s. d.	s. d.	s. d.
1875–76	3 0	3 0	5 0	7 6	1899	12 6	12 0	10 0	10 6
1877	4 0	4 0	4 0	—	1900	8 0	10 6	10 6	17 6
1878	5 0	5 0	6 0	7 6	1901	10 0	9 0	5 0	17 6
1879	6 0	6 0	8 0	6 6	1902	7 0	7 6	7 6[3]	15 0
1880	6 6	—	7 6	7 6	1903	9 0	12 6	14 0	15 0
1881	6 0	10 0	10 0	—	1904	10 0	7 6	9 0	10 0
1882	7 6	10 0	5 0	10 0	1905	6 0[4]	10 0	12 6	8 0[5]
1883	10 0	5 0	7 0	8 0	1906	12 6	12 6	12 6	15 0
1884	8 0	12 0	25 0	25 0	1907	8 0	8 6	15 0	18 0
1885	12 0	7 6	15 0	17 6	1908	7 0	9 0	14 0	12 6
1886	10 6	12 0	13 0	12 6	1909	12 0	17 0	14 0	16 6
1887	7 0	8 0	12 0	27 0	1910	11 0	11 0	7 0	12 6
1888	15 0	24 0	20 0	18 0	1911	9 6	9 6	9 6	10 0
1889	11 0	16 0	19 0	11 0	1912	8 6	25 0	12 6	15 0
1890	11 0	9 0	9 0	9 0	1913	14 0	7 6	6 0	13 0
1891	10 0	9 6	17 0	7 6	1914	13 0	17 0	25 0	19 0
1892	6 6	4 6	8 0	8 0	1915	17 0	12 6	10 0	11 0
1893	5 0	11 0	6 0	9 0	1916	10 0	12 0	15 0	19 0
1894	12 0	12 0	13 0	8 0	1917	14 0	9 0	12 6	16 6
1895	15 0	8 6	10 0[1]	12 0	1918	20 0	14 0	21 0	19 0
1896	9 0[2]	6 6	7 6	27 6	1919	12 6	11 6	17 6	13 0
1897	10 0	8 6	9 0	12 6	1920	10 9	7 6	9 0	11 0
1898	3 0	6 0	12 0	14 0	1921	9 0	8 0	7 6	9 6

[1] Supplement 1s. 6d. additional.
[2] Supplement 2s. 6d. additional.
[3] Supplement 3s. additional.
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[5] Supplement 2s. 6d. additional.

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	s. d.	s. d.	s. d.	s. d.	s. d.
1922	2 6	13 6	11 0	13 0	2 0
1923	2 6	12 0	16 0	13 6	2 0
1924	2 0	13 6	12 6	10 0	2 0
1925	2 0	12 0	8 9	14 6	2 0
1926	2 0	13 6	9 6	15 0	2 0
1927	2 6	10 6	14 0	12 3	2 0

Year.	Part 1.	Part 2.	Part 3.	Part 4.	Part 5.	Part 6.
	s. d.	s. d.	s. d.	s. d.	s. d.	s. d.
1928	2 0	8 6	8 9	10 0	9 0	2 0
1929	2 0	6 3	8 6	11 0	12 6	2 0
1930	2 0	10 0	8 9	8 6	16 3	2 0
1931	2 0	8 0	7 0	7 3	8 9	2 0

Year.	Parts 1–2.	Parts 3–4.	Parts 5–6.
	s. d.	s. d.	s. d.
1932 ..	6 6	9 6	8 6
1933 ..	8 0	11 9	8 6
1934 ..	6 6	8 6	10 9
1935 ..	7 9	10 3	11 3
1936 ..	6 6	7 0	9 9
1937 ..	6 0	9 3	8 9
1938 ..	6 3	11 6	9 9
1939 ..	12 3	12 3	8 9
1940 ..	11 9		

INDEX TO VOLUMES I-L OF THE PROCEEDINGS [Issued 15th February, 1929]. Pages 108. Price 5s.

The MACLEAY MEMORIAL VOLUME [Issued 13th October, 1893]. Royal 4to, ii and 308 pages, with portrait, and forty-two plates. Price £2 2s.

DESCRIPTIVE CATALOGUE OF AUSTRALIAN FISHES. By William Macleay, F.L.S. [1881]. A few copies only. Price £1 net.

The TRANSACTIONS OF THE ENTOMOLOGICAL SOCIETY OF NEW SOUTH WALES, 2 vols., 8vo. [Vol. I (complete in five parts, 1863-66), price 70s. net, Parts 2-5 10s. each; Vol. II (complete in five parts, 1869-73), price 30s. net, or single Parts 7s. 6d. each.]

PROCEEDINGS, 1940, PARTS 1-2.

CONTENTS.

CORRIGENDUM.

Page xx, line 12, *for* Algebunga, *read* Alberga

(Issued 16th September, 1940.)

Vol. LXV.
Parts 3-4.

Nos. 289-290.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1940.

Parts III–IV (Pages 211–420).

CONTAINING PAPERS READ IN MAY-AUGUST.

With eight plates.

[Plates vi-xiii.]

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The Linnean Society of New South Wales

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1884	8 0	12 0	25 0	25 0	1907	8 0	8 6	15 0	18 0
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1886	10 6	12 0	13 0	12 6	1909	12 0	17 0	14 0	16 6
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1891	10 0	9 6	17 0	7 6	1914	13 0	17 0	25 0	19 0
1892	6 6	4 6	8 0	8 0	1915	17 0	12 6	10 0	11 0
1893	5 0	11 0	6 0	9 0	1916	10 0	12 0	15 0	19 0
1894	12 0	12 0	13 0	8 0	1917	14 0	9 0	12 6	16 6
1895	15 0	8 6	10 0[1]	12 0	1918	20 0	14 0	21 0	19 0
1896	9 0[2]	6 6	7 6	27 6	1919	12 6	11 6	17 6	13 0
1897	10 0	8 6	9 0	12 6	1920	10 9	7 6	9 0	11 0
1898	3 0	6 0	12 0	14 0	1921	9 0	8 0	7 6	9 6

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1923	2 6	12 0	16 0	13 6	2 0
1924	2 0	13 6	12 6	10 0	2 0
1925	2 0	12 0	8 9	14 6	2 0
1926	2 0	13 6	9 6	15 0	2 0
1927	2 6	10 6	14 0	12 3	2 0

Year.	Part 1.	Part 2.	Part 3.	Part 4.	Part 5.	Part 6.
	s. d.	s. d.	s. d.	s. d.	s. d.	s. d.
1928	2 0	8 6	8 9	10 0	9 0	2 0
1929	2 0	6 3	8 6	11 0	12 6	2 0
1930	2 0	10 0	8 9	8 6	16 3	2 0
1931	2 0	8 0	7 0	7 3	8 9	2 0

Year.	Parts 1–2.	Parts 3–4.	Parts 5–6.
	s. d.	s. d.	s. d.
1932 ..	6 6	9 6	8 6
1933 ..	8 0	11 9	8 6
1934 ..	6 6	8 6	10 9
1935 ..	7 9	10 3	11 3
1936 ..	6 6	7 0	9 9
1937 ..	6 0	9 3	8 9
1938 ..	6 3	11 6	9 9
1939 ..	12 3	12 3	8 9
1940 ..	11 9	10 6	

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FOR THE YEAR

1940.

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1880	6 6	—	7 6	7 6
1881	6 0	10 0	10 0	—
1882	7 6	10 0	5 0	10 0
1883	10 0	5 0	7 0	8 0
1884	8 0	12 0	25 0	25 0
1885	12 0	7 6	15 0	17 6
1886	10 6	12 0	13 0	12 6
1887	7 0	8 0	12 0	27 0
1888	15 0	24 0	20 0	18 0
1889	11 0	16 0	19 0	11 0
1890	11 0	9 0	9 0	9 0
1891	10 0	9 6	17 0	7 6
1892	6 6	4 6	8 0	8 0
1893	5 0	11 0	6 0	9 0
1894	12 0	12 0	13 0	8 0
1895	15 0	8 6	10 0[1]	12 0
1896	9 0[2]	6 6	7 6	27 6
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1903	9 0	12 6	14 0	15 0
1904	10 0	7 6	9 0	10 0
1905	6 0[4]	10 0	12 6	8 0[5]
1906	12 6	12 6	12 6	15 0
1907	8 0	8 6	15 0	18 0
1908	7 0	9 0	14 0	12 6
1909	12 0	17 0	14 0	16 6
1910	11 0	11 0	7 0	12 6
1911	9 6	9 6	9 6	10 0
1912	8 6	25 0	12 6	15 0
1913	14 0	7 6	6 0	13 0
1914	13 0	17 0	25 0	19 0
1915	17 0	12 6	10 0	11 0
1916	10 0	12 0	15 0	19 0
1917	14 0	9 0	12 6	16 6
1918	20 0	14 0	21 0	19 0
1919	12 6	11 6	17 6	13 0
1920	10 9	7 6	9 0	11 0
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1922	2 6	13 6	11 0	13 0	2 0
1923	2 6	12 0	16 0	13 6	2 0
1924	2 0	13 6	12 6	10 0	2 0
1925	2 0	12 0	8 9	14 6	2 0
1926	2 0	13 6	9 6	15 0	2 0
1927	2 6	10 6	14 0	12 3	2 0

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1928	2 0	8 6	8 9	10 0	9 0	2 0
1929	2 0	6 3	8 6	11 0	12 6	2 0
1930	2 0	10 0	8 9	8 6	16 3	2 0
1931	2 0	8 0	7 0	7 3	8 9	2 0

Year.	Parts 1–2.	Parts 3–4.	Parts 5–6.
	s. d.	s. d.	s. d.
1932 ..	6 6	9 6	8 6
1933 ..	8 0	11 9	8 6
1934 ..	6 6	8 6	10 9
1935 ..	7 9	10 3	11 3
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1937 ..	6 0	9 3	8 9
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