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THE  
PROCEEDINGS  
OF THE  
LINNEAN SOCIETY  
OF  
NEW SOUTH WALES

FOR THE YEAR

1946

VOL. LXXI.

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WITH NINETEEN PLATES.

255 Text-figures and 1 Map.

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SYDNEY:

PRINTED AND PUBLISHED FOR THE SOCIETY BY  
AUSTRALASIAN MEDICAL PUBLISHING CO. LTD.,  
Seamer Street, Glebe, Sydney,

and

SOLD BY THE SOCIETY.

1946

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## ANNUAL GENERAL MEETING.

WEDNESDAY, 27th MARCH, 1946.

The Seventy-first Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 27th March, 1946.

Dr. Ida A. Brown, President, in the Chair.

The minutes of the preceding Annual General Meeting (28th March, 1945) were read and confirmed.

## PRESIDENTIAL ADDRESS.

Since the last Annual General Meeting of the Society a year ago we have seen the cessation of hostilities after the greatest armed conflict the world has ever witnessed. We hope that the forces which have brought war to a successful conclusion will prevail to restore law and order, and that eventually there will be established "on earth peace, goodwill toward men".

Many of our members have been engaged on national service, most of them applying their specialized knowledge and training to the war effort. Some have seen active service, and all but one of these—Dr. Consett Davis, a former Linnean Macleay Fellow—have returned safely and are again taking their places in the scientific community. We welcome them back among us and wish them all success.

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

Owing to a protracted strike of printing trade employees in the latter half of 1945, followed by power restrictions which extended into 1946, Parts 3-4 of Vol. lxx of the PROCEEDINGS, which should have been printed on 15th September, 1945, were not issued until 15th February, 1946, and it will be some months before Parts 5-6 will be printed.

Exchanges received from scientific societies and institutions totalled 670 for the year, compared with 749, 878 and 664 for the three preceding years. Since the cessation of hostilities a number of enquiries have been received from institutions on the foreign exchange list and in a few instances exchange relations have been resumed. It is, therefore, to be expected that the exchanges received next year will show a marked increase. During the year the following institutions have been added to the exchange list: Rothamsted Experimental Station, the All-Union Lenin Library, Moscow, and the Institute of Plant Industry, Leningrad.

An interesting feature during the year has been the very marked increase in the purchase of back volumes of the PROCEEDINGS by overseas libraries, especially in the United States of America.

In April, 1945, a special meeting was held to confirm the alterations to the Society's rules, which were approved at a special meeting held in the preceding month, and which were designed to expedite the admission of new members and to provide for the holding of ordinary meetings at such place and time as shall be decided by the Council.

In May, 1945, Mr. A. R. Woodhill was re-elected to the Council to fill the vacancy caused by the resignation of Mr. W. H. Maze.

Since the last Annual Meeting the names of nine new members have been added to the list, four Ordinary Members and one Honorary Member have been lost by death and three have resigned.

Edmund John Allen, who died on 9th February, 1946, was born at Mackay, Queensland, on 17th July, 1868. He spent many years of his life in northern Queensland in the Construction Branch of the Queensland Railways. Throughout his life he was keenly interested in natural history, especially entomology, the study of dragon-flies being one of his chief hobbies. He collected insects in the Cairns district with the late

Dr. R. J. Tillyard and maintained a correspondence with both Dr. Tillyard and the late Mr. A. M. Lea. He had been a member of the Society since 1905.

Archdeacon F. E. Haviland, who died on 14th August, 1945, in his 87th year, was an Ordinary Member of the Society from 1911 until 1943, when he was unanimously elected a Corresponding Member of the Society in recognition of his contributions in the field of botany.

Edward Sutherland Stokes, who died on 12th April, 1945, at Lindfield, had been a member of the Society since 1905. From 1904 to 1935 and again for a short period, 1942-43, Dr. Stokes was Medical Officer to the Metropolitan Water, Sewerage and Drainage Board. He was a recognized authority on the chemistry and bacteriology of water.

Frank Henry Taylor, who died at Epping on 20th December, 1945, was born at Lakemba on 12th July, 1886. From 1906 to 1911 Mr. Taylor was a scientific cadet in the New South Wales Public Service. In 1911 he was appointed Entomologist at the Australian Institute of Tropical Medicine, Townsville, Queensland. In 1930 he became Lecturer in Entomology at the School of Public Health and Tropical Medicine, The University of Sydney, a position which he occupied at the time of his sudden death.

Mr. Taylor carried out a number of surveys of insect-carriers of disease, especially in northern New South Wales, Queensland and New Guinea, and the results of these surveys were published in a number of Science Bulletins. Mr. Taylor began collecting insects at an early age, concentrating on the Diptera, especially the Culicidae, in which family he described many new species. For many years Mr. Taylor was the recognized authority on Australian mosquitoes and he published a number of taxonomic papers on this group, and on other insects of medical importance, in these PROCEEDINGS and various overseas scientific journals.

Mr. Taylor joined the Linnean Society in 1907 and was one of its most enthusiastic members. He became a member of the Council in 1937 and was President during 1942-43. He was also a Fellow of the Royal Entomological Society of London and the Zoological Society of London. A number of entomologists in Australia owe their first interest in the subject to Taylor's enthusiasm. He was ever ready to help these younger workers and spent much time in the Society's library checking references and abstracting papers for entomologists stationed in country districts and in other States.

James Thomas Wilson, emeritus Professor of Anatomy in the University of Cambridge, died at Cambridge on 2nd September, 1945, in his eighty-fifth year.

Wilson came to Australia to occupy the position of demonstrator in Anatomy in the University of Sydney, and in 1890, when the Chair was established, he became the first Challis Professor of Anatomy. He held this position for thirty years and during this time built up a very fine department, and in addition to his teaching work, carried out much fundamental research work on monotremes and marsupials, his scientific researches securing for him election to a Fellowship of the Royal Society in 1909. It was during this period that Professor Wilson took such an interest in this Society. He became a member in 1892 and was made an Honorary Member in 1923. He served on the Council from 1893 to 1900, and again from 1906 to 1912, being President during 1897-1899.

In 1920 he was appointed to the Chair of Anatomy in the University of Cambridge, a position which he occupied until his retirement in 1934. Older members of the Society speak in glowing terms of Professor Wilson's ability as a teacher and research worker, and of his many charming personal qualities.

Reference may here be made to the death of Mr. Arthur Francis Basset Hull, M.B.E., F.R.Z.S., on 22nd September, 1945, at the age of eighty-two years. Mr. Basset Hull was a member of this Society from 1907 to 1940, a member of Council for approximately twenty-five years of this period and President in 1923-24. Commencing in 1909 he published many zoological papers in these PROCEEDINGS and other scientific journals.

Mention may also be made of the death of John Shewan on 30th March, 1945, at the age of eighty-eight; he was for many years in charge of the collections in the Macleay Museum at the University of Sydney.

I have pleasure in informing you that, in response to representations from the three owner-bodies, the Government has agreed to make available the land adjoining Science

House in York Street for extension of the building, provided that in any such extension the Government's requirements for the whole area are complied with.

During the year the Wild Flowers and Native Plants Protection (Amendment) Bill was passed by the State Government with the object of preventing the further despoliation of our native flora.

The Sir Joseph Banks Memorial Bill was also passed by the State Government during the year. This terminated the Sir Joseph Banks Trust, vested the Fund in the Trustees of the Public Library of N.S.W., for the purpose of editing and publishing the Sir Joseph Banks Papers, and stipulated that the residue of the Fund, if any, after publication of the Banks Papers, together with the proceeds from the sales of the publication, be used for publishing works in the natural sciences with special reference to Australasia.

Following discussions between representatives of the Kosciusko State Park Trust and members of a Scientific Advisory Committee composed of representatives of the Royal Zoological Society of N.S.W. and of this Society, the Trust agreed to meet the expenses for a party of eight scientists for a period of one month at Kosciusko in order to carry out a reconnaissance natural history survey. The survey party, which included six members of this Society and consisted of zoologists, botanists, geologists and a geographer, left Sydney in mid-January and returned in mid-February. Very satisfactory results were achieved and this survey can now form the basis of further detailed work.

We offer congratulations to Lieutenant G. A. V. Stanley, R.A.N.V.R., on the award of the Distinguished Service Cross in recognition of sustained courage and endurance and "skill of a standard beyond the ordinary course of duty under most hazardous conditions in the Aitape-Wewak area", and to Dr. A. H. Voisey and to Dr. J. A. Dulhunty on attaining the degree of Doctor of Science of the University of Sydney.

Mrs. D. M. Frith, B.Sc.Agr., who had been assistant to the Macleay Bacteriologist, Dr. H. L. Jensen, from 1st July, 1943, resigned on 30th September, 1945, and another assistant has not yet been appointed.

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

Dr. H. L. Jensen, Macleay Bacteriologist to the Society, has continued experiments on the influence of hydrogen ion concentration on symbiotic nitrogen fixation in lucerne and subterranean clover. The rate of nitrogen fixation in sand media at different pH-levels has been compared with the rate of uptake of combined nitrogen (nitrate or ammonia). The experiments have shown as a general result that the infection of the roots by the nodule bacteria, and consequently the number of root nodules formed, is influenced chiefly by the reaction, but the mass of the nodule tissue chiefly by the nitrogen supply. The nitrogen-fixing efficiency of the nodule tissue in lucerne is lowered at pH 5 and less, but the process of fixation still continues at pH 4.6-4.8 and in subterranean clover even at pH 4.2-4.5. Supply of combined nitrogen reduces the weight and especially the nitrogen-fixing efficiency of the nodule tissue in both plants. The uptake of combined nitrogen is generally less strongly influenced by the reaction than is the process of nitrogen fixation. Experiments on the influence of molybdenum on symbiotic nitrogen fixation have shown that, in order to fix nitrogen at an optimal rate, the nodule substance must contain a certain concentration of molybdenum several times higher than that of the rest of the plant tissues. A paper on this subject is awaiting publication.

Dr. Jensen's work on mould-proofing of military equipment has been concluded and a short paper on the activity of certain fungicidal substances is being prepared. Dr. Jensen's co-operation in this work throughout the war years through the intermediary of the Scientific Liaison Bureau has been highly praised by the Director of the Tropical Deterioration Information Centre, U.S.A., and the Australian Minister for the Army.

During the first six months of her Fellowship year Dr. Germaine A. Joplin, Linnean Macleay Fellow of the Society in Geology, was granted leave of absence in order to carry out teaching duties in the Department of Geology of the University of Sydney, but during her leave period she completed some work previously commenced on the highly siliceous slates of the Upper Ordovician, and a paper on the results of this work was published in these PROCEEDINGS. This study pointed to the high silica content of these rocks being original, and it was suggested that the rocks were of tuffaceous origin, the tuff

showers entombing and preserving the graptolites which are so characteristically present in this rock type. Since re-commencing her Fellowship work in September, Dr. Joplin has continued detailed petrological work on the Albury Complex both in the field and in the laboratory, and these results are now being embodied in a paper which will be submitted for publication within the next few months. The Ordovician metamorphic and igneous rocks show close similarity to those of Cooma, but as they represent only the peripheral part of the large Victorian Complex, certain conclusions regarding them must be left until more detailed work is carried out in Victoria. It appears likely that the Victorian Complex is surrounded by zones similar to those recognized and mapped at Cooma, but as this area possibly represents a higher level of the intrusion, certain differences are apparent when the two areas are compared. Thus, at Albury a zone of sills is superimposed upon several of the high-grade metamorphic zones and these have superimposed a retrograde metamorphism. Younger granites, possibly representing Silurian, Middle Devonian and Kanimbla intrusions, have added a further complication by superimposing their contact effects.

During the past year Miss Frances M. V. Hackney, Linnean Macleay Fellow of the Society in Plant Physiology, carried out further investigations on the respiratory metabolism of developing Granny Smith apples and of mature Granny Smith apples after various periods of cool storage. Further data were obtained regarding the effects of addition of possible respiratory substrates and respiratory inhibitors to apple tissue. Possible respiratory substrates included succinic, malic and citric acids, polyphenol compounds and ascorbic acid. The extent to which these substances affected the respiration rate depended to a great extent on the maturity of the apples used. Possible respiratory inhibitors used were cyanide malonate and resorcinol. The results indicated that approximately fifty per cent. of the respiration of cut apple tissue (skin or flesh) was due to the activity of a cyanide-insensitive system. There was a good deal of evidence that polyphenol oxidase and succinic dehydrogenase played important parts in the respiratory metabolism; ascorbic oxidase might also have been important. The presence of an enzyme capable of oxidizing reduced cytochrome was demonstrated, but the possible importance of this enzyme in apple respiration requires further investigation.

Mrs. Joan M. Beattie (*née* Crockford), Linnean Macleay Fellow of the Society in Palaeontology, continued the description of Upper Palaeozoic Bryozoa, dealing with the Carboniferous and Permian faunas of New South Wales and Queensland. The early part of the year was spent in dealing with a fauna of Permian age from Lake's Creek in the Rockhampton district of Queensland; this fauna, comprising mainly fenestrate Bryozoa, was found to have affinities with both the Eastern and Western Australian Permian faunas and with the Permian Bryozoa of Timor. A paper dealing with the Lake's Creek fauna was read at the July meeting of the Society and has since been published in these PROCEEDINGS. The greater part of the year has been spent in a study of the Lower Carboniferous faunas of New South Wales and Queensland. Very few species belonging to these faunas, which are large and varied, have previously been described; a paper dealing with them and comparing them with the Permian faunas found in Eastern and Western Australia is in course of preparation.

Only two applications for Linnean Macleay Fellowships were received in response to the Council's invitation of 26th September, 1945. I have pleasure in reminding you that the Council reappointed Miss Frances M. V. Hackney to a Fellowship in Plant Physiology for one year from 1st March, 1946, and appointed Miss June Lascelles, B.Sc., to a Fellowship in Biochemistry for one year from 1st March, 1946.

Miss June Lascelles graduated in Science at the University of Sydney in 1945 with the University Medal and First Class Honours in Biochemistry. She was awarded a Commonwealth Research Grant and worked in the Department of Biochemistry, and at the end of March, 1945, became a Teaching Fellow in the same department. As a fourth year student Miss Lascelles commenced an investigation of the oxidation of molecular hydrogen by heterotrophic bacteria. Some of the results obtained in 1944 were summarized in a letter to the Editor of the *Australian Journal of Science*, January, 1945, by Dr. J. L. Still and Miss Lascelles. During 1945 this work was continued and a paper incorporating the results is in course of preparation.

During the coming year Miss Hackney proposes to carry out further investigations on the effects of various concentrations of possible respiratory substrates and various concentrations of respiratory inhibitors on the respiratory metabolism of Granny Smith apples. Special attention will be given to the effects of maturity and of time in cool store on the responses of the tissues to various treatments.

Miss Lascelles proposes to continue her work on the oxidation of molecular hydrogen by bacteria. Molecular hydrogen can be utilized for the biological reduction of a number of compounds involved in the economy of micro-organisms and Miss Lascelles will continue the study of these reductions in four genera of heterotrophic micro-organisms—*Clostridium*, *Escherichia*, *Azotobacter* and *Proteus*.

We wish them success in their coming year's work.

At the close of this session we shall lose two members of Council who have given long years of service to the Society; Mr. C. A. Sussmilch, who retires, does not seek re-election, and the resignation of Mr. E. C. Andrews from the Council was accepted, with regret, at the last Council meeting. To both of these gentlemen I wish to express the appreciation of the Society for their valuable services.

#### AN OUTLINE OF THE HISTORY OF PALAEOLOGY IN AUSTRALIA.

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#### 1. INTRODUCTION.

For the second part of my address I have chosen a subject which I hope may be of general interest to members and of some value to geologists.

Recently there has been awakened interest in the history of Sciences in Australia, and that of palaeontology is more or less typical of the so-called natural sciences. There are certain well-defined stages common to them all. In the first half of the nineteenth century there were maritime surveys such as those led by Flinders, Baudin, Stokes and Wilkes, which, although primarily geographical survey-expeditions, included in their personnel a naturalist or scientist who collected botanical, zoological and geological specimens and returned with them to the Northern Hemisphere. Later came individual collectors, some independent, others attached to inland exploratory expeditions, who by collecting for museums or by sending material to specialists in Europe for description and publication, made known to the world some of the peculiarities of the past and present fauna and flora of Australia.

About the middle of the century commenced the foundation of Universities, Royal Societies and other Scientific Organizations and the establishment of State Departments such as the Geological Surveys; these have given opportunity to a great number of trained scientists, the results of whose researches have appeared in numerous publications.

The formation of the Australasian Association for the Advancement of Science in 1888 was the first successful attempt to co-ordinate research in this country, and its twenty-four meetings since that time have been of inestimable value in bringing together workers in similar fields from places scattered over the Commonwealth. Its more recent service (following on the work of the Australian National Research Council) of the publication of "Science Abstracts" as a supplement of the *Australian Journal of Science* is of great benefit to the scientific worker in giving an index of scientific work published in or on Australia.

General accounts of the history of geology and geologists in Australia in the nineteenth century have been given already by R. Tate (1893), E. J. Dunn (1910), E. W. Skeats (1934), E. C. Andrews (1943) and others. Also the "Catalogue of Australian

Fossils" by R. Etheridge, junr. (1878), the "Catalogue of Geological Works on the Australian Continent" by Etheridge and Jack (1881), and various other bibliographies and historical introductions to specialized papers contain a wealth of information on the geology and palaeontology up to the time of their publication. Nevertheless, there are certain aspects of palaeontology to which, so far, no reference has been published. Being a biological science, palaeontology is bound by the International Rules of Nomenclature, by which primary type-specimens are of the greatest importance in evaluating specific names. Since the collectors of the nineteenth century discovered many of the commonest species of Australian fossils, which were named and were often imperfectly described and figured, it has become necessary, for the proper identification of these species, to trace the whereabouts of the actual specimens collected, and also to ascertain their original locality for topotype material. The first descriptions were published in English or foreign journals and the specimens are scattered in museums the world over, or are completely lost. On a visit abroad during 1938-39 I was fortunately able to trace some of these old collections.

## 2. THE STATUS OF PALAEOLOGY ELSEWHERE IN THE EARLY NINETEENTH CENTURY.

It may be well to consider briefly the status of palaeontology elsewhere in the early part of the nineteenth century, when the first Australian collections were being made.

From very early times fossils had been known to man; the early Egyptians, the Greeks and the Romans all recognized the petrified remains of plants and animals, but it was not until the eighteenth century that there was any real appreciation of their significance. During the eighteenth century useful work was carried out in the publication of descriptions and figures of fossils. Baldassari (1751), like Leonardo da Vinci before him, realized that fossils do not occur indiscriminately scattered through the rocks but are in groups or families, and that lithological and palaeontological facies differences occur. Buffon (1707-1788) recognized that a succession of faunas and floras had taken place, and various workers attempted to distinguish successive bands of stratified rocks by the fossils they contained. However, it was left to William Smith, "the Father of English Geology", to establish by his map (1815) and his paper (1816) the "law of superposition" of strata and to enunciate the "principle of faunal dissimilarity", which form the basis of stratigraphical geology.

The work of Smith, Cuvier, Lamarek and others in the early nineteenth century is generally recognized as the real foundation of scientific palaeontology. Thereafter fossils were considered from two different points of view: (1) stratigraphical, as "time-markers" or indicators of geological age and (2) biological, as individual forms of life, related to one another in time and space.

The stratigraphical aspect was first developed by several English geologists, who have since become world-famous. In 1831 Sir Roderick Murchison commenced to apply the principles of William Smith to the series of sediments underlying the Coal Measures of England, and he was able to work out a regular succession of shales and limestones with distinctive fossils. In 1835 he defined the Silurian System, which he described in great detail in 1839. In the meantime, Prof. Sedgwick worked on what he considered to be an older series in north-west Wales, which in 1835 he defined as the Cambrian System. Later it was found that there was some overlap of the Systems as defined by these workers and the Ordovician System was proposed by Prof. Lapworth in 1874 to avoid confusion. It was not until 1900 that the name "Ordovician" was adopted officially by the Geological Survey of New South Wales.

Murchison and Sedgwick established the Devonian System in 1840. "Carboniferous" was in common usage for the coal-bearing formations of the English Midlands.

In 1841, following two visits of Murchison to Russia, the Permian System was defined for rocks in the "ancient kingdom of Permia", near Moscow, which were younger than the Coal Measures of England.

The post-Palaeozoic terms were also introduced about this time, Triassic by F. von Alberti in 1834, Jurassic by A. Brongniart in 1829 and Tertiary by G. Cuvier and H. Brongniart in 1810.



It is a tribute to the soundness of the work of these pioneers that the major subdivisions of the geological record, which they established, have since been found to have world-wide application.

The field-men worked in close collaboration with the palaeontologists of the day; great collections of fossils were made in England, Europe and elsewhere, and these were described in a fine series of monographs of various palaeontographical societies and other special publications.

Thus it can be seen that the development of the science was proceeding simultaneously with the discoveries being made in the new continent.

### 3. MARITIME AND INLAND SURVEYS.

Although some geological observations had been made on earlier expeditions, it was not until the voyage of Matthew Flinders (1801–1803) that specimens of fossils were collected from Australia by the well-known botanist on the expedition, Robert Brown. In 1821 the Rev. Dean W. Buckland reported on these specimens, "impressions of leaves of ferns" from the Hunter River district, and Upper Palaeozoic marine shells, including a spirifer, from "Table Mountain, near Hobart's Town, Van Diemen's Land". Apparently Charles Stokes, a member of the Council of the Geological Society of London, acquired this collection of fossils and presented it to the Society in May, 1821; in 1911 it was transferred to the British Museum (Nat. Hist.), where it still remains.

In 1825 Koenig named the spirifer from this collection as the type of a new species and a new genus, *Trigonotreta stokesii*, in honour of his friend, Charles Stokes, and this appears to be the first published description of a fossil from Australia.

The fossil plants collected by R. Brown and mentioned by Buckland appear to be those that Alex. Brongniart (1828) described and named as *Glossopteris Browniana* and *Phyllothea australis* from the Newcastle Coal Measures, New South Wales. This is the first record of palaeobotanical material from Australia, although coal had been discovered near South Cape (Tasmania) by La Billardière, botanist to the D'Entrecasteaux Expedition of 1792–3, and also south of Sydney, in New South Wales, and in the banks of the Hunter River during Flinders' explorations in 1797.

Another botanist, Allan Cunningham, collector for Kew Gardens, discovered the Ipswich Coal Measures on the Brisbane River in 1828 and must have noted the presence of fossil plants.

The discovery of Tertiary fossils in limestones of the Lower Murray Valley was made by C. Sturt in 1829, on his expedition down the Murrumbidgee River to the mouth of the Murray.

The next work of palaeontological interest is that of Sir Thomas L. Mitchell. Before properly setting out on his first inland expedition towards the end of 1831, he discovered and collected marine (Permian) fossils on the banks of the Hunter River, "26 miles from the sea" (= Harper's Hill). These included seven species, all new, which were named and described by J. de C. Sowerby. This was the initiation of the work on the Upper Palaeozoic marine faunas of Eastern Australia, which even at the present time is far from completion.

Mitchell also discovered fossiliferous limestone (Carboniferous), near the present site of Somerton, in 1831.

In 1830 Mitchell examined the caves in the limestone of Wellington, New South Wales, previously discovered by Oxley, and found in them the remains of Pleistocene marsupials, *Diprotodon* sp. and *Macropus* sp., which were afterwards described by Sir Richard Owen. This was the beginning of a long series of works from 1843 to 1880 by Owen on Tertiary and Post-Tertiary mammals, culminating in his monograph "On the Fossil Mammals of Australia, Parts i-x".

Mitchell also noticed (1838) in the vicinity of the "Coodradigbee River" limestones with corals, which he correlated with "Mr. Murchisson's Silurian System" (now known to be Lower and Middle Devonian).

Charles Darwin visited Australia in 1836 as naturalist on the *Beagle* under Captain Fitzroy, R.N. In the vicinity of Hobart he collected Permian marine fossils and Tertiary leaves, and the specimens were taken to England for examination. The Bryozoa

("corals") were described by W. Lonsdale and the brachiopods by G. B. Sowerby (1842). Unfortunately the specimens appear to have been lost, and I was unable in 1938 to trace the whereabouts of any of them, although search was made for them at all likely places, including Down House Museum (Darwin's old home), the British Museum and the Museums at Cambridge and Liverpool.

Probably the most valuable of the early geological work in the continent was that of Count P. E. de Strzelecki. His book, entitled "The Physical Description of New South Wales and Van Diemen's Land", was published in 1845, after five years of exploration in "New South Wales" (Eastern Australia) and Tasmania, including travelling on foot for 7,000 miles. His map is the oldest published geological map of any part of Australia. There is an important section of the book devoted to the description of the fossil faunas and floras, over fifty Palaeozoic species, mostly new, being described by the English palaeontologists W. Lonsdale and J. Morris. A few specimens come from limestone now known to be Silurian in New South Wales, but the majority are those forms most common in the Permian of New South Wales and Tasmania; a few Pliocene species were described by G. B. Sowerby, and descriptions of *Diprotodon* sp. and *Nototherium* sp. by R. Owen are quoted. The specimens of invertebrate fossils are now in the British Museum (Nat. Hist.) and plaster casts of some of these were generously presented to the Department of Geology of the University of Sydney in 1939.

Another notable explorer, Dr. Ludwig Leichhardt, who had received geological training in Europe, records in the journal of his expedition from Moreton Bay to Port Essington in 1844-1845 the presence of coal on the Mackenzie and Bowen Rivers, and of plant remains in other parts of northern Queensland. He also discovered limestone on the Burdekin River, now known to be of Middle Devonian age, but the specimens which he collected, including fossils, had to be abandoned on the journey. A list of the fossils he collected in 1842-43, published in Waugh's Almanac, is quoted by Clarke (1878, p. 120).

The United States Exploring Expedition under, Charles Wilkes, which visited Sydney in 1839-1840, carried as naturalist J. D. Dana, who collected fossil specimens from the Wollongong district. Descriptions of these were not published until 1849. The fossil types are now in the United States National Museum, Washington, D.C., and the duplicates and plastotypes are in the Peabody Museum, Yale University.

The last of the maritime surveys which is of interest to us here is that of H.M.S. *Fly*, on which J. Beete Jukes, Geological Surveyor for Newfoundland, was official naturalist. His geological observations were published in several papers and a book (1850). His paper (1847) "Notes on the Palaeozoic Formations of New South Wales and Van Diemen's Land" describes the stratigraphy and lists collections of fossils from Wollongong and the Hunter River in New South Wales and from various Permian localities in Tasmania. The specimens mentioned in this paper are now in the British Museum (Nat. Hist.), having been transferred from the Geological Society's Museum (London) in 1911.

#### 4. INDIVIDUAL WORKERS.

For more than a hundred years valuable contributions have been made to the science by men who were either not professional palaeontologists or who were not employed by scientific organizations as palaeontologists, but who had a keen interest in natural history and the collection of fossils. Some of the finest specimens in Museums were collected by these men, who counted not the cost in time and labour in developing a complete or rare specimen.

The oldest and best known of these men was Rev. W. B. Clarke, "the Father of Australian Geology". He was a trained geologist, having studied under Prof. Sedgwick at Cambridge, and before leaving England had published several geological papers. An account of his life and work has recently been given by J. Jervis (1944).

From the time of his arrival here in 1839 to his death in 1878, he travelled widely over New South Wales, making geological observations in the course of his clerical duties. He had one brief visit to Tasmania. He kept up a correspondence with Sedgwick, Murchison, McCoy and other leading geologists of his time and met a number of explorers and visiting geologists, including Leichhardt, Jukes, King, Strzelecki, Dana and others. He also had contact with the Macleays, to whom this Society owes so much:

Most of the papers relating to the life and work of W. B. Clarke are available in the Mitchell Library, Sydney, and reference need be made here only to his palaeontological work. In seeking to elucidate the stratigraphy of his adopted country he made huge collections of fossils, which he sent to England and Belgium for identification and description. The first collection of over 2,500 specimens was sent to Sedgwick at Cambridge in 1844, and the Upper Palaeozoic forms were studied by McCoy, whose work was published in 1847. In this important paper 20 species of plants and 83 species (including 40 genera) of animals were described, about half of them as new species. Although W. B. Clarke maintained that the marine fossils and the fossil plants from the associated coal measures belonged to the same geological period, McCoy regarded the plants as much younger ("Oolitic" or Jurassic). This was the beginning of a long controversy between McCoy and Clarke on the age of the Hunter River Coal Measures, which should have been easily settled had the palaeontologist seen the field-evidence.

Clarke presented the collection described by McCoy to the Woodwardian Museum, Cambridge, where it still remains. Before despatching it, Clarke made pencil sketches of about 2,000 of the specimens in three note-books, to which he refers in the 4th Edition (1878) of his book "Sedimentary Formations of New South Wales", published shortly before his death. By some happy chance these sketch-books escaped destruction in the Garden Palace Fire in Sydney in September, 1882, when many of his specimens and other notes were lost. These books are valuable in giving clues to the localities of specimens which are otherwise obscure from McCoy's published records. Incidentally Clarke mentions that some of the fossils come from "on" or "near the Mount Wingen fault", a feature rediscovered many years later, and he also gives drawings of objects from Glendon and Darlington (near Singleton), which were long afterwards described under the name of "glendonites" by David *et al.* (1904).

Further collections of fossils were sent to Cambridge by Clarke, but for some time no one was available to study them. By 1864 arrangements were made with Prof. L. G. de Koninck, of the University of Liège, Belgium, for the description of these Australian fossils, and 1876-1877 saw the publication of de Koninck's monumental work as part of the *Memoires de la Société royale des Sciences de Liège*, 2nd Ser., Vol. ii. In this, de Koninck described as Silurian 59 species, as Devonian 81 species and as Carboniferous 176 species, many of which were new. This work, written in French, was translated by Prof. and Mrs. T. W. E. David and Mr. W. S. Dun and was republished in 1898 as a Memoir of the Geological Survey of New South Wales, Palaeontology No. 6. The specimens studied by de Koninck were returned to Clarke but subsequently were all lost in the Garden Palace Fire in Sydney in 1882.

Clarke's collection of fossil plants, mainly from the Coal Measures, was sent in 1876 to Dr. Feistmantel, then palaeontologist to the Geological Survey of India, who was studying plants of similar age in India. Feistmantel's work was published in *Palaeontographica* in 1878-1879 on his return to Europe and was later translated and republished as a Memoir of the Geological Survey of New South Wales, Palaeontology, No. 3, in 1890. In this work the *Rhacopteris* flora of New South Wales and the *Glossopteris* and Mesozoic floras were described.

The works of de Koninck and Feistmantel were undoubtedly among the most important contributions to Australian palaeontology prior to 1880.

Although Clarke collected mainly from the Middle and Upper Palaeozoic of New South Wales, he also discovered fossils at Wollumbilla, Queensland, in 1860, which were determined as Mesozoic.

Clarke himself had a very facile pen: a bibliography of his geological works has been given by Etheridge and Jack (1881). In the fourth edition of his book, "Sedimentary Formations of New South Wales", published shortly before his death in 1878, he gave an admirable summary, not only of his own researches, but of much that was known at that time of the stratigraphy and palaeontology of Eastern Australia.

Another unofficial palaeontologist of note was Rev. J. E. Tenison-Woods. His palaeontological work was chiefly on the Tertiary fossils of South Australia, Victoria, Tasmania and New Guinea, and he published over forty books and papers on this subject, eleven of them in the PROCEEDINGS of this Society (1877-1880).

An active worker in several branches of sciences, who published a great number of papers (103), was R. M. Johnston. He was Government Statistician and Registrar-General of Tasmania from 1881-1918 but never held an official position as geologist. He will long be remembered as the author of the great work "A Systematic Account of the Geology of Tasmania", published in 1888. Economic geology plays a large part in this book; it also contains a splendid account of the stratigraphy of the Island and lists of fossils determined by Etheridge, junr., and others are quoted. It is illustrated by over 50 plates of fossils. The specimens are mostly in the Museums of Hobart and Launceston; some are in the British Museum (Nat. Hist.). Although overdue for revision, very few of these specimens have been redescribed to date.

Following these men were a number who by collecting fossils made valuable contributions to our knowledge of palaeontology. Among them may be mentioned C. Jenkins, who made extensive collections of Silurian fossils in the Yass-Bowning district. His specimens are in the University of Sydney and the Australian Museum. His three papers on the Geology of Yass Plains were published by this Society in 1878 and 1879. He was followed by J. Mitchell, who made extensive collections in the Silurian and Devonian in the Yass district and in the Carboniferous north of Newcastle. He worked in collaboration with Etheridge, junr., and published a number of papers, some in these PROCEEDINGS. Yet another ardent collector in the Yass district, Mr. A. J. Shearsby, who happily is still with us, has done valuable work for over forty years since his first contact with Prof. David and R. Etheridge at a University Camp near Yass in 1901. He also has published papers in these PROCEEDINGS and his collections are in Museums in Sydney, Melbourne and elsewhere.

Valuable and extensive collections of Permian marine fossils made by J. Waterhouse, senr., Varney Parkes and others are housed in the Australian Museum, Sydney.

In Victoria similar work has been done by collectors such as George Sweet and F. A. Cudmore. In Western Australia, specimens collected by W. W. Froggatt in North-Western Australia on behalf of Sir William Macleay were described by Etheridge in 1889, again in these PROCEEDINGS.

The Rev. W. Howchin, later Lecturer in Palaeontology and subsequently Professor in the University of Adelaide, commenced his geological career as an amateur.

It is impossible to mention all who have contributed and are still contributing to this work. Their patient, unselfish and enthusiastic efforts have been a big factor in advancing our knowledge of the palaeontology and stratigraphy of Australia.

##### 5. GEOLOGICAL SURVEYS, UNIVERSITIES AND MUSEUMS.

About the middle of last century the need for the development of mineral resources, especially with the discovery of gold in payable quantities and the consequent increase in size and wealth of the community, led to the establishment of the Geological Surveys, the Universities and Museums.

The subsequent development of the palaeontology and stratigraphy of Australia may be divided into three stages:

- i. 1852-1892, the period from the establishment of the first of the official Geological Surveys and the Universities to the publication of Jack and Etheridge's "Geology and Palaeontology of Queensland and New Guinea", which gave an important summary of geological knowledge of Eastern Australia;
- ii. 1892-1932, a period of great development in most of the States, ending with another grand summary in the form of David's "Explanatory Notes to a New Geological Map of the Commonwealth"; and
- iii. 1932-present time (1946), a period of more or less intensive specialization.

##### i. First Period, 1852-1892.

The early history of the Geological Survey of New South Wales is recorded in the Legislative Assembly Papers collected as a volume "Papers Relative to Geological Surveys", New South Wales (including Queensland), 1851-1870. A summary of the history of the Queensland Survey is given by Jack and Etheridge (1892, pp. v-xvii)

and of the other States and the Universities by Andrews (1943). Biographical sketches of the early members of the Surveys and related information have been given by Dunn (1910), Skeats (1934) and others.

The University of Sydney, although established in 1852, had no special lecturer in palaeontology until 1902, but the University of Melbourne was fortunate in securing in 1855, as one of its four foundation Professors, Frederick McCoy, already an eminent British palaeontologist, who had published descriptions of some of the collections of W. B. Clarke. McCoy was appointed Palaeontologist to the Geological Survey of Victoria in 1856 and was the founder and Director of the Museum of Natural History and Geology in Melbourne. The high standard of palaeontological work which has been maintained since in Victoria owes much to the influence of Prof. (later Sir Frederick) McCoy. He has left a wonderful record of published research in English journals, in his "Prodromus of the Palaeontology of Victoria", and in the *Proceedings of the Royal Society of Victoria*. His palaeontological work, which he continued until only a few months before his death in 1899, covered a wide range of subjects, but was mainly on Palaeozoic and Cainozoic faunas.

McCoy was the only official palaeontologist in Australia until the appointment in 1876 of Ralph Tate as the first Elder Professor of Natural Science in Adelaide. Tate's palaeontological researches were chiefly on the Tertiary of South Australia and Victoria. He named and described over 200 species of Tertiary Mollusca, his collections forming the Tate Collection in the University of Adelaide. To him goes the honour of the discovery in 1879 of fossiliferous Cambrian rocks in South Australia.

In his Inaugural Address to the Australian Association for the Advancement of Science at Adelaide in 1893, he gave an account of the early history of geological work in Australia and a documented summary of all the important discoveries and original researches on palaeontology and stratigraphy in this country up to the year 1892, which makes it unnecessary to consider here the work of this period in detail.

Special mention may be made of the publication of important researches on Tertiary floras by Baron von Mueller (1876, see Singleton, 1941) and by Baron von Ettingshausen, whose work was translated and republished as a Monograph of the Geological Survey of New South Wales, Palaeontology No. 2, in 1888.

E. T. Hardman, Government Geologist of Western Australia, collected specimens from the Kimberley district, Western Australia, in 1883, and the fossils were described by A. H. Foord, H. A. Nicholson and G. J. Hinde in 1890. These specimens are in the British Museum (Nat. Hist.) London, as are also those of Upper Palaeozoic fossils of New South Wales and Tasmania mentioned by W. Keene (1865, 1866).

R. Etheridge, senr., described Daintree's Collection of Palaeozoic and Mesozoic fossils of Queensland in 1872 and his son, R. Etheridge, junr., studied Australian fossils collected by R. L. Jack and others from about 1874, while still working at the British Museum. He had been engaged as a field-geologist on the Geological Survey of Victoria, but returned to England in 1871 and published a score of palaeontological papers before his return to Australia in 1887, when he took up his appointment as Palaeontologist to the Geological Survey of New South Wales and the Australian Museum.

He reported on fossils from all States of Australia and Tasmania, and in 1888 commenced writing a series of Palaeontological Memoirs published by the Geological Survey of New South Wales. He published a large number of papers in these PROCEEDINGS from 1888 onwards.

He collaborated with R. L. Jack in "The Geology and Palaeontology of Queensland and New Guinea", which was written mainly before his return to Australia. The main bulk of Etheridge's work, however, falls into the next period.

The publication of Jack and Etheridge's work, and of Tate's admirable Inaugural Address, and the subsequent appearance of new workers in the fields of Ordovician and Tertiary research in Victoria make the year 1892 a convenient date to close the first period of official palaeontology in Australia.

#### ii. *Second Period, 1892-1932.*

This period was one of great progress, during which all the principal fossiliferous areas in Australia were examined, at least in a preliminary way. There was a marked

increase in the number of workers in all States, particularly in Victoria, and greater facilities were provided for the publication of research by the State Geological Surveys, Museums, Royal Societies and other scientific organizations.

The outstanding figure of this period in Australian palaeontology, especially in its early part, was R. Etheridge, junr., a brief account of whose life has been given by Dun (1926). From the time he took up official duties as Palaeontologist in Sydney in 1887 until his death in 1920 he accomplished an amazing amount of scientific work chiefly on palaeontology and ethnology.

His palaeontological work, based on his experiences in the British Museum, covered a wide range of subjects, dealing with faunas and floras of all geological ages, and he described fossils from all States of Australia. He gradually removed some of the early handicaps to research in this country—lack of comparative fossil material and palaeontological literature—by exchange with overseas workers and built up one of the finest palaeontological libraries in the Commonwealth at the Australian Museum, Sydney. Although he was called on to identify great numbers of specimens collected by field-officers of the Surveys, most of his work was done with meticulous care and in the best traditions of the science. The revisions of the forms he described, which become necessary from time to time, are due to advances in general knowledge and methods of research and reflect in no way on the magnificent work he carried out. His bibliography of 355 original and 57 joint works and papers compiled by W. A. Rainbow (1926) includes a number of major publications. Among these may be noted his monograph on Palaeozoic corals of New South Wales, and many papers on the rugose corals of Lilydale, Yass, Taemas, Tamworth, Orange, Wellington, Rockhampton, Chillagoe and elsewhere; similar monographs and papers on Upper Palaeozoic and Cretaceous Mollusca, particularly the lamellibranchs; and other works on fossil vertebrates—fishes, reptiles, birds and mammals.

The specimens Etheridge described are housed either in Museums in the State of origin or in the Australian Museum, Sydney.

Some of the other researches carried out during this period may be considered conveniently under the headings of the States.

In Western Australia, following on Etheridge's efforts, F. W. Whitehouse published work on Jurassic fossils and on Permian faunas. Some detailed studies of Devonian and Permian fossils, particularly the brachiopods, were made by Lucy Hosking. Also certain forms considered to have stratigraphical significance, the tooth of a shark, *Helicoprion davisii*, and the goniatite now known as *Metalegoceras jacksoni* were studied and re-studied in attempts to effect correlation of the Western Australian Upper Palaeozoic with strata elsewhere.

In South Australia the faunas of the Tertiary formations claimed the attention of Tate, Howchin, Chapman and others. In the classic work of T. Griffith Taylor on the Cambrian Archaeocyathinae, published as a Memoir of the Royal Society of South Australia in 1910, a high standard of palaeontological research was attained. Other Cambrian fossils such as the trilobites and brachiopods were also the subjects of investigation.

Victoria can claim the greatest number of trained and active palaeontologists during this period. By 1892 it was known that graptolites occurred abundantly in certain parts of Victoria, having been discovered by the first field-officers of the Victorian Geological Survey from 1856 on, and identified by McCoy, but up to this time the stratigraphical sequence had not been worked out. In the year 1892 T. S. Hall commenced his long series of researches on the graptolites, paying special attention to the stratigraphical correlation of the Victorian formations with occurrences elsewhere. He was soon joined by G. B. Pritchard, the two working together on Ordovician and also on Tertiary faunas for the next quarter of a century. Besides being of academic interest, the Ordovician work has been of great economic value, as the graptolite zones have been used to work out the structure of the gold-fields of Bendigo, Ballarat and Castlemaine. Two other notable palaeontologists later joined in the work on Victorian graptolites, W. J. Harris in 1916 and R. A. Keble in 1920, and their work still continues.

Statements of the progress of research on the graptolitic facies of Victoria to the close of our second period have been given by David (1932) in his "Explanatory Notes" and by Harris and Keble in a paper to the Royal Society of Victoria in 1931.

F. Chapman came to this country in 1902 to take up his official position as Palaeontologist to the National Museum, Melbourne. Later he was appointed Palaeontologist to the Geological Survey of Victoria and part-time Lecturer in Palaeontology at the University of Melbourne. Before his arrival in Victoria he had become an authority on the Foraminifera, on which he had published a text-book. In his official capacity he was called on to identify an overwhelming number of fossils of all kinds and ages, and he published descriptions of many rare and previously unknown fossil forms from Australia. That much of his work stands in need of revision by modern methods of research should in no wise obscure the fact that he made a magnificent contribution to Australian palaeontology. The two principal fields of his research were the faunas of the shelly facies of the Silurian of Victoria and New South Wales, the Devonian of Victoria and the more recent fauna of the Tertiary period, particularly the Foraminifera and Mollusca. The bibliography of his published work shows the scope and the importance of his contributions. To him is due also the awakened interest of a number of students of palaeontology whose main work falls into the next period.

Other noteworthy researches on the Tertiary of Victoria include those of W. Howchin on the Foraminifera and of P. H. MacGillivray and C. M. Maplestone on the Bryozoa.

There were few official palaeontologists in New South Wales during this period; maybe the quality and quantity of work they achieved offset their lack of numbers! The prolific researches of R. Etheridge, junr., up to about 1920 have already been mentioned. J. Mitchell, an unofficial palaeontologist, collaborated with Etheridge in the publication of a series of papers on Silurian trilobites from 1890 to 1917 in these PROCEEDINGS.

The scientific work of W. S. Dun almost exactly covers the second period of our history. He was appointed in 1892 as an assistant to Etheridge and later succeeded him on the Geological Survey, the two publishing papers in collaboration during the early part of their association. He was appointed visiting Lecturer in Palaeontology at the University of Sydney in 1902, in which capacity he acted until his death in 1934. As with the other official palaeontologists of this time, Dun was called on to enter many fields of palaeontology and palaeobotany, though perhaps his best work was on the marine faunas of the Upper Palaeozoic of New South Wales. His results were published chiefly in the Records of the Geological Survey of New South Wales and the Records of the Australian Museum. His influence went far beyond his publications and he was ever ready to help those who needed assistance in research.

W. N. Benson published in 1921-1922 two valuable papers on Palaeozoic faunas, one on the Devonian palaeontology of Australia, the other on the Lower Carboniferous fauna of New South Wales, and these were followed in 1923 by a more philosophical paper on "Palaeozoic and Mesozoic Seas in Australia" dealing, *inter alia*, with the succession of faunas.

Other work of the period includes that of F. W. Booker on Palaeozoic brachiopods, H. O. Fletcher on Mollusca and R. J. Tillyard on Permian insects.

In the palaeobotanical field A. B. Walkom made notable contributions to our knowledge of the Upper Palaeozoic and Mesozoic floras of New South Wales, although his principal work was done in Queensland, where his palaeobotanical studies (1915-1922) led to the more exact separation of freshwater beds of Triassic, Jurassic and Cretaceous age and to a better knowledge of the Palaeozoic floras.

F. W. Whitehouse (1926-1928) established zones in the marine Cretaceous of Eastern Australia on the basis of his studies of the Ammonoidea. The Mesozoic of Queensland has yielded a marvellous series of fossil insects, some of which were studied by R. J. Tillyard during his tenure of a Linnean Macleay Fellowship in Zoology. His work, originally published in these PROCEEDINGS (1917-1923), was re-issued as Publication No. 273 of the Queensland Geological Survey.

J. H. Reid (1930) gave a valuable paper entitled "The Queensland Upper Palaeozoic Succession" summarizing and adding to our knowledge of the stratigraphy and palaeontology of Queensland.

Few major studies of Tasmanian fossils were made during this period. Small collections of marine fossils were described by R. Etheridge, junr. and W. S. Dun, and of Mesozoic plants by A. B. Walkom (1925).

The close of the second period was marked by the publication of Sir T. W. E. David's "New Geological Map of the Commonwealth" and the accompanying "Explanatory Notes", which not only gave a condensed summary of the stratigraphical and palaeontological work—official and unofficial—accomplished until then, but incidentally revealed many of the gaps in our knowledge.

### iii. *Third Period, 1932 to Present Time (1946).*

Since 1932 very considerable advances have been made, especially within the last 10 years. Over 400 papers on Australian stratigraphy and palaeontology have been published, some of them works of major importance. Authors from all States have contributed, all geological periods have been dealt with and many different fossil-groups have been studied. There has been a greater tendency towards specialization, and this will undoubtedly increase with time. The general trend has been towards much more accurate field-work and the mapping of palaeontological horizons, and more careful collection and identification of fossils. Comparisons with similar forms in other parts of the world have made possible more precise correlation with strata elsewhere.

It is impossible to discuss here all the advances which have been made, but a few will be mentioned under the headings of the geological systems. References to the original papers will be found easily in "Science Abstracts" from 1932 on.

*Cambrian.*—Field-work on the Cambrian of Central and South Australia has been carried out by C. T. Madigan, D. Mawson and others; R. and R. J. Bedford have published accounts of new forms of Archaeocyathinae.

F. W. Whitehouse has done important field-work in western and north-western Queensland, and his masterly study of the Trilobita has made possible the zoning of the rocks here. Primitive Echinodermata have been described and work on the Brachiopoda is in progress.

*Ordovician.*—The studies of the Victorian palaeontologists W. J. Harris and R. A. Keble were continued and they were joined in the work by D. E. Thomas. A valuable series of papers has been published, including one by Harris and Thomas in 1938, "A Revised Classification and Correlation of the Ordovician Graptolite Beds of Victoria". A complete bibliography and history of research on graptolites in Australia by R. A. Keble and W. N. Benson (1939) makes further comment here unnecessary. The extension of Lower Ordovician graptolite-bearing rocks into New South Wales at Narrandera has been proved, and a Victorian-trained geologist, Mrs. K. M. Sherrard, has discovered Upper Ordovician graptolites east of Yass, New South Wales. G. F. K. Naylor has also made new discoveries of Upper Ordovician graptolites in New South Wales.

The recognition by C. Teichert of *Bathmoceras*, an Ordovician zone fossil, in the Larapintine Series of Central Australia has permitted correlation with the graptolite-bearing Darriwilian Series of Victoria.

The trilobite beds at Junee and Caroline Creek in Tasmania, previously regarded as Cambrian, have been shown to be probably basal Ordovician by Kobayashi, and this is likely to be confirmed by other studies now in progress. W. H. Bryan (1944) has found an Upper Ordovician graptolite at Upper Brookfield in the Brisbane Schist Series, thus contributing to the very vexed question of the age of the Series.

*Silurian.*—A great deal of field and laboratory work has been carried out on this system in Eastern Australia and some fifty papers published thereon. Zonal mapping has been done of the shelly facies of the Yass district, New South Wales, and of the graptolitic facies in various parts of Victoria, and several attempts at correlation of the two facies have been made by Chapman, Thomas, Harris and Gill in Victoria.

G. F. K. Naylor has found Silurian graptolites in the Goulburn district of New South Wales and Mrs. Sherrard's discovery of graptolites of the zones 26 to 35 of the



English succession in a bed overlying the Silurian limestones and the middle trilobite (*Dalmanites*) bed of the Yass sequence is of particular significance. Other references to researches on the graptolites will be found in Keble and Benson's Catalogue.

Some detailed palaeontological work has been done on the shelly fossils. Valuable studies have been made of corals by Dr. D. Hill and O. A. Jones, of Echinodermata by Chapman, Withers and Keble, of brachiopods by F. W. Booker, Joan Johnston and J. K. S. St. Joseph, of somewhat rare Bryozoa by Joan Crockford and of Trilobita by E. D. Gill.

Dr. Isabel Cookson's descriptions of the Silurian *Baragwanathia* flora are noteworthy, these being the oldest recorded land-plants in the world.

The age of the Yeringian Lilydale Limestone and associated shales has been the subject of intensive research by several workers. From her study of the stromatoporoids E. Ripper was convinced that the Limestones were of Lower Devonian age; this was strongly supported by Dr. Hill after studying the Rugosa. Careful collecting in the type area of Lilydale has been carried out by E. D. Gill, who has published a series of papers on the fauna of the shales, which he maintains are also of Lower Devonian age. Whether the other occurrences in Victoria, which are at present correlated with the Yeringian, are also of Lower Devonian age is a matter which has yet to be investigated. The fallacy of many such correlations in the past has been due to comparisons of lists of fossil-names, without critical comparisons of the actual specimens.

*Devonian*.—Considerable advances have been made in our knowledge of this system during recent years. A number of areas has been mapped, some in detail, although much zonal work remains to be done both in Eastern and in Western Australia.

Outstanding palaeontological work includes that of E. S. Hills on Middle and Upper Devonian fishes, and of E. Ripper on stromatoporoids, reef-building organisms of importance here both in the Silurian and the Devonian. A masterly study of the Rugose corals by Dr. D. Hill and of the Heliolitida and Tabulata by D. Hill and O. A. Jones has made possible the correlation of all the main outcrops of Lower and Middle Devonian limestones in Eastern Australia.

The description of goniatites from Mt. Pierre, Western Australia, and their reference to zones in the Belgian succession by G. Delépine has been followed by C. Teichert's comprehensive palaeontological and stratigraphical work on the Upper Devonian of Western Australia.

*Carboniferous*.—Relatively few papers have been published on this system since 1932, but some of these have had far-reaching implications. D. Hill has shown that all the Carboniferous Rugosa of New South Wales and Queensland belong to the lower part of the System.

S. W. Carey's work on a complete sequence of Carboniferous beds in the Werrie Basin, New South Wales, and a study of some of the fossils by G. Delépine and others has led to the correlation of several zones in New South Wales with zones in the standard English and Belgian sequences, and this in turn to the recognition of facies variations in the marine and freshwater deposits from about the middle of the Lower Carboniferous on.

An interesting series of Carboniferous plants and seeds has been described by A. B. Walkom.

*Permian*.—Studies of various aspects of the Permian problem in Australia have been popular since the days of W. B. Clarke, and are no less so at the present time, some 80 papers having been published on the subject since 1932.

Among the major field-studies of recent years may be mentioned those of H. G. Raggatt and of C. Teichert in the North-West Basin of Western Australia; of L. J. Jones in the Cessnock area, and of A. H. Voisey and J. A. Dulhunty elsewhere in New South Wales.

Most of the fossil groups have come under revision of recent years and much research is in progress. The Foraminifera (chiefly arenaceous forms) have been dealt with by Chapman, Howchin and Parr, and by I. Crespin; the Rugosa by D. Hill; the Bryozoa by J. Crockford; the Brachiopoda by K. L. Prendergast and others; and the Pelecypoda by

- WALKOM, A. B., 1918.—*PROC. LINN. SOC. N.S.W.*, 43 (1): 37-115.  
 ———, 1922.—*Qd. Geol. Surv.*, Publ. No. 270.  
 ———, 1925.—*Pap. Proc. Roy. Soc. Tasm.* for 1924: 73-89.  
 ———, 1926.—*Ibid.* for 1925: 63-74.  
 WHITEHOUSE, F. W., 1926.—*Mem. Qd. Mus.*, 8 (3): 195-242.  
 ———, 1927.—*Ibid.*, 9 (1): 109.  
 ———, 1928.—*Ibid.*, 9 (2): 200.  
 WOODS, J. E. T., 1877-1880.—*PROC. LINN. SOC. N.S.W.*, Vols. 2-5.

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The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 28th February, 1946, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.); and he moved that they be received and adopted, which was carried unanimously.

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

*President:* A. R. Woodhill, B.Sc.Agr.

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

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

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

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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			
Contingencies Reserve .. .. .	20,000	0	0			
	9,216	3	1			
Accumulated Funds .. .. .	29,216	3	1			
Commercial Banking Company of Sydney Ltd. .. .. .	66	10	0			
Suspense .. .. .	15	0	0			
Current Liabilities .. .. .	81	10	0			
	<hr/>			<hr/>		
	£29,297 13 1			£29,297 13 1		

ASSETS.

	£	s.	d.	£	s.	d.
Fixed Assets—						
Commonwealth Loan, at cost .. .. .	500	0	0			
Debentures: Metropolitan Water, Sewerage and Drainage Board, at cost .. .. .	494	7	6			
Society's Freehold, at cost .. .. .	11,000	0	0			
Science House (one-third share), at cost .. .. .	14,715	0	0			
Loan on Mortgage .. .. .	2,500	0	0			
	<hr/>			<hr/>		
29,209	7	6				
Current Assets—						
Income Account .. .. .	78	5	7			
Cash in hand .. .. .	10	0	0			
	<hr/>			<hr/>		
	88			5 7		
	<hr/>			<hr/>		
	£29,297 13 1			£29,297 13 1		

INCOME ACCOUNT. Year Ended 28th February, 1946.

	£	s.	d.	£	s.	d.
To Balance from 1944-45 .. .. .	620	18	8			
" Salaries .. .. .	939	3	4			
" Printing Publications .. .. .	121	11	0			
" Illustrations .. .. .	95	8	11			
	<hr/>			<hr/>		
" Rates and Insurance .. .. .	216	19	11			
" Postage .. .. .	327	16	8			
" Petty Cash .. .. .	42	6	3			
	<hr/>			<hr/>		
" Audit .. .. .	22	19	4			
" Printing .. .. .	10	10	0			
" Expenses .. .. .	11	15	6			
" Expenses (16 College Street) .. .. .	41	14	2			
" Attendance and Cleaning .. .. .	30	2	6			
" Library .. .. .	26	0	0			
" Pay-roll Tax .. .. .	63	4	5			
" Bank Expenses .. .. .	3	3	9			
	<hr/>			<hr/>		
	187			6 10		
	<hr/>			<hr/>		
	£2,357 11 0			£2,357 11 0		
By Subscriptions: 1945-46: .. .. .				£	s.	d.
Arrears .. .. .				134	8	0
In advance .. .. .				11	11	0
	<hr/>			<hr/>		
				155	8	0
" Entrance Fees .. .. .				9	9	0
" Interest .. .. .				170	3	11
" Rent .. .. .				551	18	8
" Science House .. .. .				597	0	0
" Sales (including 60 copies of PROCEEDINGS purchased by Government of N.S.W.) .. .. .				200	19	4
" Fellowships Account (surplus income at 28th February, 1946, transferred) .. .. .				594	6	6
" Balance to 1946-47 .. .. .				78	5	7
	<hr/>			<hr/>		
				£2,357	11	0

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1946, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1946, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1946.

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

4th March, 1946.

A. B. WALKOM,  
Hon. Treasurer.

**LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.**  
BALANCE SHEET at 28th February, 1946.

	£	s.	d.		£	s.	d.
<b>LIABILITIES.</b>				<b>ASSETS.</b>			
<b>Accumulated Funds—</b>				Fixed Assets—			
Amount bequeathed by Sir William Macleay	35,000	0	0	Commonwealth Loans, at cost	29,350	0	0
Surplus Income Capitalized	14,913	18	11	Debitures:			
				Metropolitan Water, Sewerage and Drainage Board, at cost	5,425	19	9
				Rural Bank of N.S.W., at cost	2,172	15	0
				Inscribed Stock:			
				Metropolitan Water, Sewerage and Drainage Board, at cost	1,005	0	0
				Loans on Mortgage	11,950	0	0
				Current Assets—	49,903	14	9
				Commonwealth Savings Bank	10	4	2
					£49,913	18	11

**INCOME ACCOUNT. Year Ended 28th February, 1946.**

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	984	7	8	By Interest	2,195	1	3
" Pay-roll Tax	14	9					
" Balance, being Surplus Income transferred to General Account	594	6	6				
" Capital Account	615	12	4				
					£2,195	1	3

**AUDITOR'S REPORT TO MEMBERS.**

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1946, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1946, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1946.

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

A. B. WALKOM,  
Hon. Treasurer.

4th March, 1946.

BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 28th February, 1947.

LIABILITIES.		ASSETS.	
	£	s.	d.
Accumulated Funds—			
Amount bequeathed by Sir William Macleay ..	12,000	0	0
Accumulated Income Capitalized ..	3,820	0	0
	15,820	0	0
Income Account at 28th February, 1947 ..	1,449	6	1
	£17,269	6	1
Fixed Assets—			
Commonwealth Loans, at cost ..			16,320
Current Assets—			
Commercial Banking Company of Sydney Ltd. ..			124
Commonwealth Savings Bank ..			818
Cash in hand ..			6
			£17,269

INCOME ACCOUNT. Year Ended 28th February, 1947.

	£	s.	d.
To Salary ..	600	0	0
Expenses ..		16	11
Petty Cash ..		1	10
Balance to 1947-48 ..	1,449	6	1
	£2,051	13	1
By Balance from 1945-46 ..			1,421
Interest ..			680
			£2,051

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1947, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1947, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1947.

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

A. B. WALKOM,  
Hon. Treasurer.  
4th March, 1947.

## ABSTRACT OF PROCEEDINGS.

### ORDINARY MONTHLY MEETING.

27th MARCH, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

The Donations and Exchanges received since the previous Monthly Meeting (28th November, 1945), amounting to 54 Volumes, 334 Parts or Numbers, 8 Bulletins, 2 Reports and 7 Pamphlets, received from 66 Societies and Institutions and 3 private donors, were laid upon the table.

#### PAPERS READ.

1. Miscellaneous Notes on Australian Diptera. xii. Cyrtidae, Dolichopodidae and Phoridae. By G. H. Hardy.
2. Studies on Australian Erythraeidae (Acarina). By R. V. Southcott, M.B., B.S.

### ORDINARY MONTHLY MEETING.

24th APRIL, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

The President announced that the Council had elected Dr. A. B. Walkom to be Honorary Treasurer for the Session 1946-47.

The President also announced that the Council had elected Mr. R. H. Anderson, Mr. E. Le G. Troughton, Dr. W. R. Browne and Dr. Ida A. Brown to be Vice-Presidents for the Session 1946-47.

Messrs. R. G. L. Brett, B.Sc., West Hobart, Tasmania, L. R. Clark, M.Sc., Canberra, A.C.T., E. F. Riek, B.Sc., Canberra, A.C.T., M. M. H. Wallace, B.Sc., Hunter's Hill, and R. H. Wharton, B.Sc., Woollahra, were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (27th March, 1946), amounting to 3 Volumes, 12 Parts or Numbers, 2 Bulletins and 1 Report, received from 11 Societies and Institutions and 1 private donor, were laid upon the table.

#### PAPERS READ.

1. Some Observations on the Plasmodia and Other Blood Parasites of Sparrows. By J. Lawrence, B.Sc.
2. Pollens of *Nothofagus* Blume, from Tertiary Deposits in Australia. By Isabel C. Cookson, D.Sc. (*Communicated by Dr. Ida A. Brown.*)

#### NOTES AND EXHIBITS.

Mr. A. Musgrave exhibited specimens and slides (prepared by Miss Gwen Burns) of an insect new to the Australian fauna—a small burrowing bug of the family Cydnidae, which, in addition to being of general interest, is of economic importance.

The original home of this insect is India and Burma, but it has now been found in the Newcastle district, New South Wales, to which locality it has doubtless been introduced through the agency of shipping.

Attention was first directed to it by Mr. A. R. Woodhill, Lecturer in Entomology, University of Sydney, to whom it was sent by Mr. T. H. Bennett. It has been established at Newcastle for about three years.

The insect has been identified as *Stibaropus molginus* (Schiödt, 1849, *Scaptocoris*), and it is also figured and described by Distant in the "Fauna of British India", Rhynchota, Vol. i, 1902, p. 84, fig. 42. An interesting feature of this little dark-chestnut

coloured bug, which measures only about nine millimetres in length, is the posterior legs, of which the femora are broad and flat, while the tibiae are rather short, stout and truncate with the margins beset by short spines. The tarsi are difficult to detect. All the legs are adapted for a burrowing mode of life.

Lefroy, in his "Indian Insect Life", 1909, p. 674, pl. lxxiii, fig. 2, points out that the "white nymphs of this insect were found by C. A. Barber at the roots of a palm in S. India at a considerable depth below the surface. They have the same burrowing legs as the adult".

Three species, in addition to *molginus*, are recorded from India by Distant: *tabulatus* Schiödte, 1849; *callidus* Schiödte, 1849; *minor* Walker, 1867.

An allied species, *S. tabulatus* Schiödte, has been recorded as a pest of the roots of tobacco in south India by P. N. Krishna Ayyar in the *Bull. Ent. Res.*, xxi (1), 1930, 29-31.

It will be appreciated that such an introduction as *Stibaropus molginus*, which is said to be destructive to the roots of grass in the Newcastle district, may prove to be an important pest in view of the apparent lack of any natural enemies.

#### ORDINARY MONTHLY MEETING.

29th MAY, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

Messrs. V. W. Holland, Vacluse, R. J. Millington, Armidale, and J. D. Tipper, A.M.I.E.Aust., Turramurra, were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (24th April, 1946), amounting to 7 Volumes, 49 Parts or Numbers, and 1 Pamphlet, received from 21 Societies and Institutions, were laid upon the table.

#### PAPERS READ.

1. The Anatomy of Two New Digenetic Trematodes from Tasmanian Food Fishes. By Peter W. Crowcroft. (*Communicated by Dr. S. W. Carey*.)
2. Catalogue of Reptiles in the Macleay Museum. Part ii. *Sphenomorphus spaldingi* (Macleay). By Stephen J. Copland, B.Sc.
3. Observations on Properties of Certain Fungicidal Compounds. By H. L. Jensen, Macleay Bacteriologist to the Society.

#### NOTES AND EXHIBITS.

Miss Elizabeth Pope exhibited a specimen and photograph of a *Chaetopterus* worm believed to be *Chaetopterus luteus* Stimpson. Only two species of *Chaetopterus* have been described from the Port Jackson region up to the present date. These are *C. luteus* of Stimpson in 1855 and *C. macropus* of Schmarda in 1861.

Schmarda's description figures the bristles of the parapodia from various regions of the body and gives a coloured illustration of the whole animal. The bristles and general appearance of the worm here submitted certainly do not correspond with Schmarda's account. The worm, however, does fit the very scanty description given by Stimpson and, since it is the common species found between tide marks and in shallow water (where Stimpson collected) in this vicinity, it seems reasonable to believe that this would be the species he collected during his visit to Sydney in December, 1853. Stimpson published no figure of this species when he described it, and we believe also that the type specimen and his notes and drawings were lost along with many other of his gatherings when fire destroyed them in 1871 when the Chicago Academy of Science was burnt. As far as is known, therefore, the photograph exhibited here, which appears on the front cover of the *Australian Museum Magazine*, Vol. ix, No. 1 (published on 15th May, 1946), is the first illustration of this species *C. luteus*. The specimen shown was collected by Miss Pope and a party of friends during February, 1946, on the mud-flats at Careel Bay, Pittwater.

Living in the tubes with the worm were numerous commensal crabs of the species *Polyonyx transversa* Hasw. A male and female of this crustacean species were also exhibited.

Mrs. A. T. Lee exhibited specimens and diagrams of *Zostera capricorni* Aschers in flower and fruit. Although fertile material of this marine Angiosperm is apparently not very rare, it is obscure and seems to have escaped observation by many collectors.

The material exhibited was collected at Pittwater in tidal water just off the Palm Beach Golf Links, on 17.iii.1945, by Dr. Lilian Fraser and the exhibitor. The dried specimens are now in the National Herbarium of New South Wales. Fragments with flowers had been found washed up further along the shore, and the extensive beds near the Golf Links were then searched for flowering plants *in situ*.

Plants in flower can usually be recognized by their more bunchy habit near the apex of the stems. The inflorescence is a spadix, enveloped by the two parallel valves of the spathe, and the flowers comprise only the essential parts—a pistil in the female flowers, an anther in the males. There are two anthers to each pistil in the spadix and each group of one female and two male flowers is subtended by a bract, a lateral, incurved extension of the spadix.

The pollen is interesting since the "grains" are long, acicular structures instead of the usual compact bodies.

Since finding this material at Pittwater fertile plants have been collected again from the same area in November and December, and in December from beds in Sirius Cove, Mosman, where the plants are exposed only occasionally at very low tides.

Mrs. F. Perrin exhibited a fine series of Tasmanian Rhodophyceae collected by herself and the late A. H. S. Lucas.

#### ORDINARY MONTHLY MEETING.

26th JUNE, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

Messrs. A. J. Bearup, Penschurst, and D. H. Colless, Manly, were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (29th May, 1946), amounting to 1 Volume, 54 Parts or Numbers, 2 Bulletins and 2 Reports, received from 25 Societies and Institutions and 1 private donor, were laid upon the table.

#### PAPERS READ.

1. A New Species of *Longetia*: The Botanical Identity of the "Pink Cherry" of Dorrigo Timber-getters. By W. A. W. de Beuzeville and C. T. White.

2. The Evolution of the Maxillo-palate. By H. Leighton Kesteven, M.D., D.Sc.

#### LECTURETTES.

Lecturettes on the natural history of the Kosciusko Area were delivered as follows:

1. Geography. By Mr. W. H. Maze, M.Sc.
2. Geology. By G. D. Osborne, D.Sc., Ph.D.
3. Botany. By Mr. F. V. Mercer, B.Sc.

#### ORDINARY MONTHLY MEETING.

31st JULY, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

Mr. P. H. Durie, B.Sc., Armidale, N.S.W., was elected an Ordinary Member of the Society.

The President referred to the death on 28th June, 1946, of Sir George Julius, who had been a member of the Society since 1930.

The President, on behalf of members, offered congratulations to Mr. F. V. Mercer on the award of a Sydney University Commonwealth Fellowship and to Mr. F. L. Milthorpe on the award of the Farrer Research Scholarship. Mr. Mercer will continue his research work at Cambridge University and Mr. Milthorpe at the University of London.

The Donations and Exchanges received since the previous Monthly Meeting (26th June, 1946), amounting to 62 Volumes, 186 Parts or Numbers, 7 Bulletins and 2 Reports, received from 39 Societies and Institutions, were laid upon the table.



## PAPERS READ.

1. Critical Notes on the Genus *Wahlenbergia* Schrader; with Descriptions of New Species in the Australian Region. By N. Lothian.
2. An Occurrence of Rhythmic Banding in Ordovician Strata of the Shoalhaven River Gorge. By Stephen J. Copland, B.Sc.
3. A Search for the Vector of *Plasmodium pteropi* Breinl. By A. J. Bearup and J. J. Lawrence.
4. Contributions to the Geology of Houtman's Abrolhos, Western Australia. By Curt Teichert, D.Sc. (*Communicated by Dr. W. R. Browne.*)

## LECTURETTES.

Lecturettes on the zoology of the Kosciusko State Park were delivered as follows:

1. Mammalogy and Conservation. By E. Le G. Troughton, C.M.Z.S., F.R.Z.S.
2. Entomology and Ornithology. By K. C. McKeown, F.R.Z.S.

## NOTES AND EXHIBITS.

Dr. W. R. Browne exhibited a series of colour photographs of the Kosciusko Area taken by Miss M. J. Colditz.

## ORDINARY MONTHLY MEETING.

25th SEPTEMBER, 1946.\*

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

Miss Mabel Crust, B.Sc., Canberra, A.C.T., and Miss Marjorie J. Wilkins, B.Sc., Mosman, were elected Ordinary Members of the Society.

The President, on behalf of members, offered congratulations to Mr. E. C. Andrews, B.A., F.R.S.N.Z., on the award of the Mueller Memorial Medal by the Australian and New Zealand Association for the Advancement of Science for his work during past years on the physiography and structural and economic geology of Australia.

The President announced that the Council is prepared to receive applications for four Linnean Macleay Fellowships tenable for one year from 1st March, 1947, 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, 1946.

The Donations and Exchanges received since the previous Monthly Meeting (31st July, 1946), amounting to 75 Volumes, 160 Parts or Numbers, 6 Bulletins, 1 Report and 4 Pamphlets, received from 59 Societies and Institutions and 3 private donors, were laid upon the table.

## PAPERS READ.

1. A Review of the Species *Catadenia carnea* R.Br. (Orchidaceae). By the Rev. H. M. R. Rupp, B.A.
2. Distribution of Microspore Types in New South Wales Permian Coalfields. By J. A. Dulhunty, D.Sc.
3. Notes on the Morphology and Biology of *Apiocera maritima* Hardy (Diptera, Apioceridae). By Kathleen M. I. English, B.Sc.
4. Notes on the Gippsland Waratah (*Telopea oreades* F.v.M.), with a Description of a New Species. By Edwin Cheel.

## ORDINARY MONTHLY MEETING.

30th OCTOBER, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

The President reminded candidates for Linnean Macleay Fellowships, 1947-48, that Wednesday, 6th November, 1946, is the last day for receiving applications.

The President, on behalf of members, offered congratulations to Dr. S. Warren Carey on his appointment to the Chair of Geology in the University of Tasmania and to Dr. N. A. Burges on his appointment to the Chair of Botany in the University of Sydney.

\* No meeting of the Society was held in August, 1946.

The Donations and Exchanges received since the previous Monthly Meeting (25th September, 1946), amounting to 12 Volumes, 135 Parts or Numbers, 8 Bulletins, 2 Reports and 7 Pamphlets, received from 43 Societies and Institutions, were laid upon the table.

## PAPER READ.

A Review of the Phylogeny and Classification of the Lepidoptera. By A. Jefferis Turner, M.D., F.R.E.S.

## LECTURE.

Life Histories of Crustacea and their Significance, with Special Reference to the Australian Penaeid Prawns. By Professor W. J. Dakin, D.Sc.

Professor Dakin's lecture dealt with the life history of Crustacea with special reference to the Penaeid prawns and the newly discovered early stages in the life cycle of the so-called Greasy Back Prawn of New South Wales. After briefly reviewing the life histories of a series of Crustacea in order to show the constancy of occurrence of the Nauplius larva, the tendency in the higher Crustacea to telescope this stage into the pre-hatching period was brought out by reference to the Decapoda.

Professor Dakin then gave a short history of the gradual discovery of the life history of the Penaeid prawns. The fact was stressed that the research in New South Wales originated in the desire to find out whether the breeding of our commercial prawns took place off shore in ocean water or inside the coastal lakes and harbours. The discovery that the King Prawn (*P. plebejus*), and very probably the School Prawn (*Metapenaeus macleayi*), always migrated to more saline ocean waters to breed, made it necessary to capture larval stages at sea, and an investigation of the complete life history was necessitated. The interesting work of a similar nature carried out during the same period by the United States Bureau of Fisheries was referred to.

In the course of the work on the King Prawn (1934); the possibility that a far less important prawn commercially (the Greasy Back) might breed within the inshore lakes was discovered. It was not until last year (1945) that confirmation of the belief seemed likely, and in the early months of this year was made certain.

Curiously enough the Greasy Back Prawn seems to have become much more important commercially (and more numerous) in recent years, especially in Tuggerah Lakes.

The breeding period occurs between December and possibly as late as May. The adult prawns are the smallest of the species commercially fished and there is a usual size difference, the larger females caught averaging four inches and the males three inches.

Original drawings and specimens were exhibited showing a Metanauplius, 1st, 2nd and 3rd Protozoal stages, Mysis and young prawn stages.

An interesting feature of the development is the gradual loss of paired spines from the telson as the post-larval stages change to the young adult form.

This would appear to be the first record of a Penaeid prawn species breeding in coastal lakes of the shallow type exemplified by Tuggerah Lakes. It is not suggested that the breeding of this particular species is confined to such waters.

It would now appear that the time has come for an exploration of the ocean bed during the summer months by fishery authorities, with a view to finding out whether or not a more extensive and more reasonable prawn fishery is possible for the mature King, School and other prawns. This was undertaken in U.S.A. waters when discoveries similar to ours had been made. The work only started in 1938 and since then a new £2,000,000 industry has been created and 50,000,000 lbs. of prawns, additional annually to the old figures, have resulted.

## NOTES AND EXHIBITS.

Mr. D. J. Lee exhibited a specimen of *Pontomyia cottoni* Wom. (Diptera, family Chironomidae) taken by Miss J. Liddell on the surface of the water in Gunnamatta Bay in 1944. This remarkable Chironomid is an aberrant type in which the secondary sexual characters of the male have been lost and the wings are malformed and no longer of use for flying. It is closely related to the Samoan *P. natans* Edw., about which more is

known. In this latter species the female is completely wingless and only two pairs of vestigial legs are present and the larval and adult life is spent submerged in tidal water in association with the marine plant, *Halophila*. So far, only the male of the Australian species, previously only known from South Australia, has been found, and it would be of considerable interest to see if the life history of *P. cottoni* followed closely that of *P. natans*.

#### ORDINARY MONTHLY MEETING.

27th NOVEMBER, 1946.

Mr. A. R. Woodhill, B.Sc.Agr., President, in the Chair.

Miss Muriel C. Morris, Newtown, and Mr. Erik Shipp, Longueville, were elected Ordinary Members of the Society.

The President announced that the Council had reappointed Miss June Lascelles, M.Sc., to a Linnean Macleay Fellowship in Biochemistry for one year from 1st March, 1947.

The Donations and Exchanges received since the previous Monthly Meeting (30th October, 1946), amounting to 4 Volumes and 19 Parts or Numbers, received from 20 Societies and Institutions, were laid upon the table.

#### PAPERS READ.

1. Description and Life History of a New Western Australian Coccid. By J. R. T. Short, B.Sc. (*Communicated by Dr. A. J. Nicholson.*)

2. Notes on Australian Orchids. v. By the Rev. H. M. R. Rupp, B.A.

3. Taxonomic Notes on the Genus *Ablepharus* (Sauria: Scincidae). i. A New Species from the Darling River. By Stephen J. Copland, B.Sc.

4. Sub-surface Peat Temperatures at Mount Kosciusko, N.S.W. By J. A. Dulhunty, D.Sc.

5. Studies on Australian Marine Algae. iii. Geographical Records of Various Species and Observations on *Acrochaetium botryocarpum* (Harv.) J.Ag. and *Pterocladia capillacea* (Gmel.) Born. and Thur. By Valerie May, M.Sc.

A short talk on plant regeneration in the Broken Hill district was given by Mr. R. H. Anderson.

#### NOTES AND EXHIBITS.

Mr. R. H. Anderson, on behalf of Dr. F. A. Rodway, of Nowra, New South Wales, exhibited botanical specimens preserved in their natural colour. Some years ago Dr. Rodway experimented with medicinal paraffin as a medium for the preservation of botanical specimens, but found that paraffin did not act as a preservative, mould soon appearing on specimens placed in it. The addition of antiseptics such as creosols, carbolic acid, chloroform, ether, etc., destroyed colouration. Recently it occurred to Dr. Rodway that thorough drying of the material would overcome the difficulty. Drying, however, must be done in such a way that the specimen does not become shrivelled and distorted, and must be done quickly so that the colours are not affected. It has been found that coarse sand gives support to the specimen during the drying process, coarse beach sand being better than fine sand as it does not tend to adhere to the specimen. The specimen is placed in a bowl and covered with the sand, and is kept warm by suspension over a very small gas flame. In this way drying is rapid, colour is retained, and the specimen then can be placed in paraffin. Specimens preserved by Dr. Rodway in September, 1946, are still in good condition.

## LIST OF MEMBERS.

(15th December, 1946.)†

## ORDINARY MEMBERS.

- 1940 Abbie, Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
- 1927 \*Albert, Michel Francois, "Boomerang", 42 Billyard Avenue, Elizabeth Bay, Sydney.
- 1940 \*Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
- 1922 Anderson, Robert Henry, B.Sc.Agr., Botanic Gardens, Sydney.
- 1899 Andrews, Ernest Clayton, B.A., F.R.S.N.Z., No. 4, "Kuring-gai", 241 Old South Head Road, Bondi, N.S.W.
- 1927 Armstrong, Jack Walter Trench, "Callubri", Nyngan, N.S.W.
- 1938 Ashby, Professor Eric, D.Sc., D.I.C., F.L.S., Botany Department, The University, Manchester, England.
- 1912 Arousseau, Marcel, B.Sc., c.o. Mr. G. H. Arousseau, 16 Woodland Street, Balgowlah, N.S.W.
- 1919 Barnett, Marcus Stanley, "The Hill", Victoria Street, Mount Victoria, N.S.W.
- 1940 Basnett, Miss Elizabeth Marie, M.Sc., New England University College, Armidale, N.S.W.
- 1935 \*Beadle, Noel Charles William, D.Sc., Botany School, Sydney University.
- 1946 Bearup, Arthur Joseph, 66 Pacific Avenue, Penshurst, N.S.W.
- 1940 Beattie, Mrs. Joan Marion, M.Sc. (née Crockford), Bradley Street, Cobar, N.S.W.
- 1907 Benson, Professor William Noel, B.A., D.Sc., F.G.S., University of Otago, Dunedin, New Zealand.
- 1941 Blake, Stanley Thatcher, M.Sc., Botanic Gardens, Brisbane, Queensland.
- 1929 Boardman, William, M.Sc., Department of Biology, University of Queensland, Brisbane, Queensland.
- 1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
- 1923 Brough, Patrick, M.A., D.Sc., B.Sc.Agr., Botany School, Sydney University.
- 1924 Brown, Miss Ida Alison, D.Sc., Department of Geology, Sydney University.
- 1941 Browne, Miss Helen Rowan, 51 Nelson Street, Gordon, N.S.W.
- 1911 Browne, William Rowan, D.Sc., Department of Geology, Sydney University.
- 1943 Bryan, Clement, B.A., Central School, Boorowa, N.S.W.
- 1931 \*Burges, Professor Norman Alan, M.Sc., Ph.D., Botany School, Sydney University.
- 1945 Burgh, Henry Bertram, 4 Rose Crescent, Mosman, N.S.W.
- 1920 Burkitt, Professor Arthur Neville St. George Handcock, M.B., B.Sc., Medical School, Sydney University.
- 1927 Campbell, Thomas Graham, Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
- 1930 Carey, Miss Gladys, M.Sc., 32 Rawson Street, Epping, N.S.W.
- 1934 \*Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
- 1905 Carne, Walter Mervyn, c.o. Department of Commerce and Agriculture, Reliance House, Flinders Lane, Melbourne, Victoria.
- 1936 \*Chadwick, Clarence Earl, B.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
- 1899 Cheel, Edwin, 40 Queen Street, Ashfield, N.S.W.
- 1932 Churchward, John Gordon, B.Sc.Agr., Ph.D., 1 Hunter Street, Woolwich, N.S.W.
- 1946 Clark, Lawrence Ross, M.Sc., c.o. Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
- 1901 Cleland, Professor John Burton, M.D., Ch.M., University of Adelaide, Adelaide, South Australia.
- 1942 Cleland, Kenneth Wollaston, M.B., Department of Anatomy, Sydney University.
- 1931 Colefax, Allen Neville, B.Sc., Department of Zoology, Sydney University.
- 1946 Colless, Donald Henry, 45A Pacific Parade, Manly.
- 1942 Copland, Stephen John, B.Sc., 7 Creewood Street, North Strathfield, N.S.W.
- 1908 Cotton, Professor Leo Arthur, M.A., D.Sc., Department of Geology, Sydney University.

† Addresses and degrees as at 28th February, 1947.

\* Life Member.

- 1928 Craft, Frank Alfred, B.Sc., 91 High Street, Taree, N.S.W.  
 1946 Crust, Miss Mabel, B.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
- 1929 Dakin, Professor William John, D.Sc., Department of Zoology, Sydney University.  
 1945 Davis, Mrs. Gwenda Louise, B.Sc., 143 Mossman Street, Armidale, N.S.W.  
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 1937 Dulhunty, John Allan, D.Sc., Department of Geology, Sydney University.  
 1926 Dumigan, Edward Jarrett, State School, Toowoomba East, Queensland.
- 1941 Edwards, Eric Thomas, Ph.D., M.Sc.Agr., National Press Pty. Ltd., 126-130 Phillip Street, Sydney.  
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 1943 Ellison, Miss Dorothy Jean, M.Sc., Abbotsleigh College, Wahroonga, N.S.W.  
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 1914 Enright, Walter John, B.A., P.O. Box 14, West Maitland, N.S.W.
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- 1935 \*Garretty, Michael Duhan, M.Sc., 477 St. Kilda Road, Melbourne, S.C. 2, Victoria.  
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 1944 Greenwood, William Frederick Neville, c.o. Colonial Sugar Refining Co. Ltd., Lautoka, Fiji.  
 1910 Griffiths, Edward, B.Sc., Department of Agriculture, Farrer Place, Sydney.  
 1936 Griffiths, Mervyn Edward, M.Sc., Australian Institute of Anatomy, Canberra, A.C.T.  
 1939 Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., Bulolo, New Guinea.
- 1939 Hackney, Miss Frances Marie Veda, M.Sc., 40 Smith Street, Summer Hill, N.S.W.  
 1925 Hale, Herbert Matthew, South Australian Museum, Adelaide, South Australia.  
 1928 Hamilton, Edgar Alexander, 16 Hercules Street, Chatswood, N.S.W.  
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 1942 Humphrey, George Frederick, M.Sc., Department of Biochemistry, Sydney University.  
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- 1917 Jacobs, Ernest Godfried, "Cambria", 106 Bland Street, Ashfield, N.S.W.  
 1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Commonwealth Forestry Bureau, Canberra, A.C.T.  
 1930 Jensen, Hans Laurits, D.Sc.Agr. (Copenhagen), Department of Bacteriology, Sydney University.  
 1945 Johnston, Arthur Nelson, B.Sc.Agr., Hawkesbury Agricultural College, Richmond, N.S.W.  
 1907 Johnston, Professor Thomas Harvey, M.A., D.Sc., F.L.S., University of Adelaide, Adelaide, South Australia.  
 1937 Jones, Mrs. Valerie Margaret Beresford, M.Sc. (*née* May), Botanic Gardens, Sydney.  
 1930 Joplin, Miss Germaine Anne, B.Sc., Ph.D., "Huyton", 18 Wentworth Street, Eastwood, N.S.W.  
 1933 Judge, Leslie Arthur, No. 1 Bridge Road, Hornsby, N.S.W.

- 1923 Kendall, Mrs. May Marston, M.Sc. (*née* Williams), 71 Victoria Road, Drummoyno, N.S.W.  
 1937 Kesteven, Geoffrey Leighton, B.Sc., Fisheries Section, C.S.I.R., Marine Biological Laboratory, Cronulla, N.S.W.  
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 1938 Kinghorn, James Roy, C.M.Z.S., Australian Museum, College Street, Sydney.
- 1939 Langford-Smith, Trevor, Ministry of Post-war Reconstruction, Canberra, A.C.T.  
 1946 Larcombe, Miss Pauline Gladys, B.Sc., 17 Ethel Street, Burwood, N.S.W.  
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 1932 Lawson, Albert Augustus, 9 Wilmot Street, Sydney.  
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 1934 Lee, Mrs. Alma Theodora, M.Sc. (*née* Melvaine), 16A Raglan Street, Mosman.  
 1945 Liddell, Miss Jean, Department of Biology, University of Adelaide, Adelaide, South Australia.  
 1943 Lothian, Thomas Robert Noel, 68 Hewitts Road, Merivale, Christchurch, N.W. 1, New Zealand.
- 1945 Mackerras, David (Private, NX 205573), Staff, 113 (Concord) Military Hospital, Concord, N.S.W.  
 1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., Veterinary Research Station, Yeerongpilly, Queensland.
- 1931 \*Mair, Herbert Knowles Charles, B.Sc., 5 Collaroy Street, Collaroy Beach, N.S.W.  
 1939 Marshall, Alan John, Department of Zoology, University Museum, Oxford, England.  
 1932 Martin, Donald, B.Sc., Box 17, Huonville, Tasmania.  
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 1932 McCulloch, Robert Nicholson, B.Sc.Agr., B.Sc., Roseworthy Agricultural College, Roseworthy, South Australia.
- 1927 McKie, Rev. Ernest Norman, B.A., The Manse, Guyra, N.S.W.  
 1944 Mercer, Frank Verdun, B.Sc., St. Andrew's College, Newtown, N.S.W.  
 1937 Middleton, Bertram Lindsay, B.A., M.D., Bridge House, Murrurundi, N.S.W.  
 1938 Miller, David, Ph.D., M.Sc., F.R.S.N.Z., F.R.E.S., Cawthron Institute, Nelson, New Zealand.  
 1946 Millington, Richard James, 65 Mann Street, Armidale, N.S.W.  
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 1939 Moye, Mrs. Joan, B.Sc. (*née* Johnston), Warragamba Dam, via Wallacia, N.S.W.  
 1926 Mungomery, Reginald William, c.o. Bureau of Sugar Experiment Stations, Department of Agriculture and Stock, Brisbane, B.7, Queensland.
- 1920 Musgrave, Anthony, F.R.E.S., Australian Museum, College Street, Sydney.
- 1939 Naylor, George Francis King, M.A., M.Sc., Dip.Ed., University of Queensland, Brisbane, Queensland.
- 1925 Newman, Ivor Vickery, M.Sc., Ph.D., F.R.M.S., F.L.S., Department of Botany, Victoria University College, Wellington, New Zealand.
- 1922 Nicholson, Alexander John, D.Sc., F.R.E.S., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
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- 1920 Noble, Robert Jackson, B.Sc.Agr., Ph.D., 32A Middle Harbour Road, Lindfield, N.S.W.  
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- 1942 O'Brien, Brian Robert Alexander, c.o. Post Office, Palm Beach, N.S.W.  
 1927 Oke, Charles George, 34 Bourke Street, Melbourne, C.I, Victoria.  
 1927 Osborn, Professor Theodore George Bentley, D.Sc., F.L.S., Professor of Botany, University of Oxford, Oxford, England.
- 1921 Osborne, George Davenport, D.Sc., Ph.D., Department of Geology, Sydney University.
- 1940 Pasfield, Gordon, B.Sc.Agr., 20 Cooper Street, Strathfield, N.S.W.  
 1922 Perkins, Frederick Athol, B.Sc.Agr., Biology Department, University of Queensland, Brisbane, Queensland.
- 1920 Pincombe, Torrington Hawke, B.A., Box 1652, G.P.O., Sydney.  
 1937 Plomley, Kenneth Francis, 50 Domain Street, South Yarra, Melbourne, Victoria.  
 1935 Pope, Miss Elizabeth Carington, M.Sc., Australian Museum, College Street, Sydney.  
 1918 Priestley, Professor Henry, M.D., Ch.M., B.Sc., Medical School, Sydney University.  
 1938 Pryor, Lindsay Dixon, M.Sc., Dip.For., c.o. Department of the Interior, Canberra, A.C.T.
- 1929 Raggatt, Harold George, D.Sc., Census Building, Canberra, A.C.T.

\* Life Member.

- 1946 Riek, Edgar Frederick, B.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
- 1936 Roberts, Noel Lee, 43 Hannah Street, Beecroft, N.S.W.
- 1932 Robertson, Rutherford Ness, B.Sc., Ph.D., Food Preservation Research Laboratory, C.S.I.R., Private Mail Bag, Homebush, N.S.W.
- 1945 Roper, Jack, M.I.H.S., 651 Williams Street, Broken Hill, N.S.W.
- 1945 Ross, Donald Ford, c.o. Ross Bros. Pty. Ltd., 545-547 Kent Street, Sydney.
- 1925 Roughley, Theodore Cleveland, B.Sc., F.R.Z.S., Chief Secretary's Department, Box 30A, G.P.O., Sydney.
- 1932 Salter, Keith Eric Wellesley, B.Sc., "Hawthorn", 48 Abbotsford Road, Homebush, N.S.W.
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- 1928 Selby, Miss Doris Adeline, M.Sc., M.B., 11 Locksley Street, Killara, N.S.W.
- 1930 Sherrard, Mrs. Kathleen Margaret, M.Sc., 43 Robertson Road, Centennial Park, Sydney.
- 1937 Simpson, Arthur Cecil.
- 1916 Smith, Miss Vera Irwin, B.Sc., F.L.S., "Loana", Mt. Morris Street, Woolwich, N.S.W.
- 1943 Smith-White, Spencer, B.Sc.Agr., 7 Merriwa Street, Gordon, N.S.W.
- 1945 Southcott, Ronald Vernon, M.B., B.S., 12 Avenue Road, Unley Park, Adelaide, South Australia.
- 1942 Spencer, Terence Edward, 16 Attunga Street, Woollahra, N.S.W.
- 1937 Spencer, Mrs. Dora Margaret, M.Sc. (née Cumpston), 16 Attunga Street, Woollahra, N.S.W.
- 1926 Stanley, George Arthur Vickers, B.Sc., c.o. Messrs. Robison, Maxwell and Allen, 19 Bligh Street, Sydney.
- 1898 Stead, David G., "Boongarre", 14 Pacific Street, Watson's Bay, N.S.W.
- 1935 Still, Jack Leslie, B.Sc., Ph.D., Department of Biochemistry, Sydney University.
- 1911 \*Sulman, Miss Florence, "Burrangong", McMahon's Point, N.S.W.
- 1944 Sykes, Stephen Myles, B.Sc.Agr., 209 Johnston Street, Annandale, N.S.W.
- 1940 Taylor, Keith Lind, B.Sc.Agr., Forestry Commission, Division of Wood Technology, 96 Harrington Street, Sydney.
- 1944 Thorpe, Ellis William Ray, B.Sc., Department of Geography, Sydney University.
- 1943 Tindale, Miss Mary Douglas, M.Sc., 60 Spruson Street, Neutral Bay, N.S.W.
- 1946 Tipper, John Duncan, A.M.I.E.Aust., Box 2770, G.P.O., Sydney.
- 1921 \*Troughton, Ellis Le Geyt, C.M.Z.S., F.R.Z.S., Australian Museum, College Street, Sydney.
- 1902 Turner, A. Jefferis, M.D., F.R.E.S., Dauphin Terrace, Brisbane, Queensland.
- 1904 Turner, Rowland E., F.Z.S., F.R.E.S., c.o. Standard Bank of South Africa, Adderley Street, Cape Town, South Africa.
- 1917 Veitch, Robert, B.Sc., F.R.E.S., Department of Agriculture and Stock, William Street, Brisbane, Queensland.
- 1930 Vickery, Miss Joyce Winifred, M.Sc., Botanic Gardens, Sydney.
- 1940 Vincent, James Matthew, B.Sc.Agr., Dip.Bact., Faculty of Agriculture, Sydney University.
- 1934 Voisey, Alan Heywood, D.Sc., New England University College, Armidale, N.S.W.
- 1909 Walkom, Arthur Bache, D.Sc., Australian Museum, College Street, Sydney.
- 1946 Wallace, Murray McCadam Hay, B.Sc., c.o. Mrs. Whelan, Sydney Buildings, Canberra, A.C.T.
- 1930 Ward, Melbourne, Pasadena Flats, Cross Street, Double Bay, Sydney.
- 1911 Wardlaw, Henry Sloane Halcro, D.Sc., F.A.C.I., Department of Physiology, Sydney University.
- 1936 Waterhouse, Douglas Frew, M.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
- 1928 Waterhouse, Lionel Lawry, B.E., "Rarotonga", 42 Archer Street, Chatswood, N.S.W.
- 1927 Waterhouse, Professor Walter Lawry, D.Sc.Agr., M.C., D.I.C., Faculty of Agriculture, Sydney University.
- 1941 Watson, Irvine Armstrong, Ph.D., B.Sc.Agr., Faculty of Agriculture, Sydney University.
- 1911 Watt, Professor Robert Dickie, M.A., B.Sc., Faculty of Agriculture, Sydney University.
- 1941 Wearne, Walter Loutit, "Telarah", 6 Collingwood Street, Drummoyne, N.S.W.
- 1946 Wharton, Ronald Henry, c.o. Department of Zoology, Sydney University.
- 1926 \*Whitley, Gilbert Percy, Australian Museum, College Street, Sydney.
- 1946 Wilkins, Miss Marjorie Jessie, B.Sc., 33 Muston Street, Mosman, N.S.W.
- 1934 Womersley, Herbert, F.R.E.S., A.L.S., South Australian Museum, Adelaide, South Australia.
- 1932 Woodhill, Anthony Reeve, B.Sc.Agr., Department of Zoology, Sydney University.
- 1936 Zeck, Emil Herman, 694 Victoria Road, Ryde, N.S.W.

\* Life Member.

## HONORARY MEMBER.

- 1923 Hill, Professor James Peter, D.Sc., F.R.S.Z., F.Z.S., F.R.S., Royal College of Surgeons,  
Lincoln's Inn Fields, London, W.C. 2, England.

## CORRESPONDING MEMBERS.

- 1902 Broom, Robert, M.D., D.Sc., F.R.S., Transvaal Museum, Pretoria, Transvaal, South Africa.  
1942 Rupp, Rev. Herman Montague Rucker, B.A., 24 Kameruka Road, Northbridge, N.S.W.  
1943 Waterhouse, Gustavus Athol, D.Sc., B.E., F.R.E.S., c.o. Australian Museum, College Street,  
Sydney.
-



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## CORRIGENDA.

## PROCEEDINGS, 1946.

Page 126, line 15 from top, for  $\text{CuSO}_4$ ,  $\text{H}_2\text{O}$  read  $\text{CuSO}_4$ , 5  $\text{H}_2\text{O}$ .

Page 126, Table 3, for Ethylmercurithiosalicyclic acid read Ethylmercurithiosalicyclic acid.

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## SOME OBSERVATIONS ON THE PLASMODIA AND OTHER BLOOD PARASITES OF SPARROWS.

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[Read 24th April, 1946.]

### INTRODUCTION.

Within a few years of the discovery of the parasite of human malaria Danilewsky found similar plasmodia in birds. Since then the study of bird malaria has proceeded fairly steadily, drawing impetus from the belief that the results obtained with the disease in birds would help to solve some of the problems of human malaria. However, little work has been done on bird malaria in Australia. Although protozoa have been found in the blood of many species of local birds, it is only rarely that plasmodia have been described. Gilruth, Sweet and Dodd (1910) found a plasmodium in the musk duck (*Biziura lobata* Shaw) and named it *Plasmodium biziurae*. This species was later found in the black swan (*Chenopsis atrata* Shaw) by Cleland (1915). Besides this, Johnston (1909) had reported finding a plasmodium in a sparrow (*Passer domesticus* Linn.). Though he described it at first as *Plasmodium praecox*, he later (Johnston and Cleland, 1909) thought that it was a new species and called it *Plasmodium passeris*. Cleland in 1915 reported finding the same species, again from a sparrow. Breinl (1913) described and figured *P. praecox* from the grey falcon (*Falco hypoleucus* Gould).

At least thirty-three species of plasmodia have been described from birds, but probably not more than fourteen of these species are valid. Four species that are usually recognized as valid have been found in the sparrow. These are *P. relictum* Grassi and Feletti, *P. cathemerium* Hartman, *P. rouxi* Sergents and Catanei, and *P. elongatum* Huff. *P. relictum* and *P. cathemerium* are common in passerine birds and have been found in many parts of the world. *P. elongatum* has also been reported from a variety of passerine birds, but is less common than the former. *P. rouxi* seems to be restricted to the sparrows of Algeria.

### METHODS.

In the present investigation the local sparrows were examined for blood protozoa, particularly the plasmodia, and an attempt was made to find invertebrate hosts of any species of the latter.

The birds were trapped alive, and smears of blood were made from the tarso-metatarsal vein, stained with Giemsa, and examined under the microscope for at least ten minutes. Usually the birds were kept for some time and blood smears were then made at intervals of a few days. In a number of cases (39), impression smears were made from some of the internal organs (liver, spleen and either bone marrow or brain) and examined as usual.

Work on the invertebrate host was confined entirely to laboratory experiments, the object of which was to determine whether certain of the local mosquitoes were susceptible to infection. Larvae or pupae of some of the local species (*Culex fatigans* Wiedmann, *Aedes (Finlaya) notoscriptus* Skuse, *Aedes (Stegomyia) aegypti* Linn., *Aedes (Pseudo-skusea) concolor* Taylor and *Anopheles annulipes* Walker) were collected in the field, larvae were reared to pupae and the adults were allowed to emerge into a mosquito cage. They were left at room temperature but the humidity was kept as high as possible. Water, and food in the form of raisins, were provided. However, before the mosquitoes were

given the opportunity to feed on an infected bird (either a canary or a sparrow), they were usually deprived of food and water for 24 hours. Two feeding methods were used. In the first, the bird was kept in the dark, confined in a small cage, in order to restrict its movements as much as possible; and there exposed to the mosquitoes overnight. The second method was that described by Huff (1927). The bird was immobilized by wrapping it in gauze and the breast region was bared by wetting and parting the feathers. The bird was then tied on top of the mosquito cage in such a way that the mosquitoes could reach the exposed breast, and left in this position for an hour. The feedings were made either in daylight or in the late afternoon in complete or semi-darkness. Any mosquitoes that engorged were isolated and kept in cages at room temperature. After 5 to 20 days they were dissected and both the mid-gut and salivary glands examined to determine whether they had become infected.

## RESULTS.

In addition to sparrows a few other birds were trapped. The results of the examination of all these birds are given in Table 1. *P. relictum* and *P. cathemerium*

TABLE 1.  
Incidence of Infection in Birds.

Species.	Number Examined.	<i>P. cathemerium-relictum.</i>	<i>Plasmodium</i> sp.	<i>Haemoproteus.</i>	"Toxoplasma."
Sparrow ( <i>Passer domesticus</i> Linn.)..	91	60	5	—	27
Blue Wren ( <i>Malurus cyaneus</i> Latham)	3	—	—	—	—
White Eye ( <i>Zosterops lateralis</i> Latham) .. .. .	3	—	—	1	—
Starling ( <i>Sturnus vulgaris</i> Linn.) ..	2	1	—	—	—
Willie Wagtail ( <i>Rhipidura leucophrys</i> Latham) .. .. .	1	—	—	—	—
Total .. .. .	100	61	5	1	27

have not been recorded separately, both species being included under *P. cathemerium-relictum* for the following reason. *P. cathemerium* was separated from *P. relictum* by Hartman (1927), who declared that the shape and arrangement of the pigment of the two species were different. This was the only morphological distinction that he made. The differences may be tabulated as follows:

*P. cathemerium.*

*Gametocytes.* Rod-shaped pigment granules which are longer and more pointed at the ends in micro- than in macro-gametocytes.

*Trophozoites.* Pigment appears as an amorphous mass, or at most not more than a few masses which are close together.

*P. relictum.*

Nearly spherical pigment granules which are usually grouped close together.

Pigment is scattered and frequently in small granules.

*P. cathemerium* is still regarded as a valid species (Bishop, 1942), but the sole morphological distinction now stressed is the difference in pigment shape in the gametocytes, particularly the microgametocytes. There is one fairly definite biological difference. Strains of *P. cathemerium* isolated from wild birds have always been synchronous, i.e., the parasites tend to keep in step, all being at the same stage of development at the same time; but the *P. relictum* strains usually show little, if any, synchronism. Occasionally synchronous strains of *P. relictum* have been isolated, but these differ from *P. cathemerium*, which liberates its merozoites in the evening, by liberating them in the morning. In a few cases smears were made at intervals throughout the day to see whether the strains were synchronous and to find the time of merozoite liberation. Two synchronous strains were found, both of the cathemerium type, i.e., liberating their merozoites in the evening. These strains were studied both in the birds

originally infected and also in canaries or sparrows inoculated from them. Similarly two asynchronous strains were carefully studied. The pigment in the gametocytes of both the synchronous and the asynchronous strains was very variable in size and in shape, at times varying from fine to coarse, and from round to somewhat elongate in the same cell. However, there seemed to be a tendency for the pigment in the gametocytes of the cathemerium strains to be more elongate than that in the relictum strains, though it was necessary to study a number of gametocytes to draw any conclusion. In fact, the two species in Sydney sparrows do not show the clear-cut morphological difference described in the literature of other countries. Since most of the birds were not given such a thorough examination, it was thought it would be less misleading if *P. relictum* and *P. cathemerium* were not separated in the results.

In some cases when the parasites were few, it was not possible to make a diagnosis beyond *Plasmodium* sp. though there is no reason to believe that these were neither *P. relictum* nor *P. cathemerium*.

Table 2 gives the results of the experimental work on the invertebrate host of *P. cathemerium-relictum*. The sixth and seventh columns give the results of the dissections on the fed mosquitoes. The result is recorded as positive if oöcytes could be seen on the mid-gut or sporozoites in the salivary glands. In most cases an asynchronous strain (*P. relictum*) was the source of the gametocytes, but similar results were obtained with a synchronous strain (*P. cathemerium*).

TABLE 2.  
*Results of Feeding Experiments with Mosquitoes.*

Species.	No. that Fed.	No. that failed to Feed.	Percentage Feds.	No. of Feds Dissected.	Number Positive.	Number Negative.
<i>Culex fatigans</i> ..	150	21	88	107	75	32
<i>Aedes notoscriptus</i> ..	27	117	19	27	0	27
<i>Aedes concolor</i> ..	1	27	4	1	1	0
<i>Aedes aegypti</i> ..	5	1	83	5	0	5
<i>Anopheles annulipes</i>	0	111	0	—	—	—

#### DISCUSSION.

A very high percentage (71%) of sparrows were infected with plasmodia; much higher than appears to have been usually found elsewhere. For instance, Manwell and Herman (1935), working at Syracuse, N.Y., found only 6 infected (all with *P. relictum*), out of 244 examined. They state that non-migratory birds like sparrows are not as commonly infected as migratory birds.

Examination of smears made from the birds at intervals of a few days often revealed infections that would otherwise have been missed. Presumably these extra positives were due to the infection being in the latent stage at first and later relapsing or, less often, to the bird being caught while still incubating the disease. On the other hand, the examination of smears from the internal organs did not reveal any infections with plasmodia that had been missed in the smears made from the tarso-metatarsal vein. These results are at variance with those of Hewitt (1940), who found more positive plasmodial infections by examining smears from the internal organs as well as from the peripheral blood.

Besides plasmodia the only other blood parasites seen in the sparrows were oval organisms that were usually found in the cytoplasm of mononuclear leucocytes, the nuclei of which they indented. Sometimes they appeared to be lying free in the blood. They were seen both in the presence of, and in the absence of, associated malaria parasites. Organisms similar to this have been frequently described. They resemble the type II avian "Toxoplasma" of Wolfson (1940) and the forms of "Toxoplasma" described and photographed by Manwell (1939). They were usually more numerous in the internal organs than in the blood from the tarso-metatarsal vein. In some cases they could be found only in the internal organs, but on the other hand, though more rarely, they might be found only in the peripheral blood.

A starling (*Sturnus vulgaris* Linn.) was found infected with *P. relictum*, which was successfully transmitted to sparrows by blood inoculation. Manwell (1934) and Manwell and Herman (1935) have reported both *P. relictum* and *P. cathemerium* from the starling in the United States of America, though they found that infections were rare.

One haemoproteus infection was found in a white eye (*Zosterops lateralis* Latham). Forms ranging from small round young forms to mature gametocytes were seen in the blood. The mature gametocytes lay beside the nucleus of the parasitized erythrocyte and encircled its ends. The pigment was coarse and tended to be rod-shaped. No schizonts were seen in smears of the liver, spleen or brain. Partial confirmation of the fact that it was not a plasmodium was obtained by inoculating blood from the white eye into a canary, which failed to develop any infection. This haemoproteus is probably identical with that described from the same species by Cleland and Johnston (1910).

It will be convenient at this point to discuss the present position of *Plasmodium passeris* described by Johnston and Cleland from a sparrow. It was originally described as *P. praecox* (Johnston, 1909). The name *P. praecox* was given by Grassi and Feletti both to a plasmodium of sparrows and to the plasmodium causing malignant tertian fever in man. These two species are quite distinct. Johnston and Cleland were unaware of this confusion in nomenclature and, since the only description of *P. praecox* available to them referred to the parasite of malignant tertian fever, they concluded that their species was new. However, this parasite of sparrows had been already described under the names of *P. praecox* and also *P. relictum* by Grassi and Feletti (1890-1891). The name *praecox* has now been generally dropped, partly owing to the confusion it has caused. The malignant tertian parasite is now called *P. falciparum* Welch, while the bird parasite is now usually known as *P. relictum* Grassi and Feletti. Since then, as has been mentioned already, a second species, *P. cathemerium*, which is closely related to *P. relictum*, has been described; the morphological distinction between them resting on differences in the pigment. The pigment of *P. passeris* was described as consisting of small granules, a description that could fit either species. *P. passeris* becomes a synonym for *P. relictum* or *P. cathemerium*.

Of the mosquitoes tested, *Culex fatigans* was by far the best vector under laboratory conditions. It would bite readily and a large proportion of the mosquitoes that fed became infected. It was hard to get the other successful vector (*Aedes concolor*) to bite. Possibly this was due to the laboratory conditions: the mosquitoes suffered a heavy mortality during the period without food and water. As they are salt-water breeders they are probably, at best, of secondary importance as a vector of the malaria parasite of sparrows in nature. *Aedes aegypti* seemed to bite birds quite readily but of the few tested none became infected. Huff (1927) has shown that they are susceptible to overseas strains of *P. relictum* and *P. cathemerium* though they are poor vectors. He found that only 6% became infected. None of the *Aedes notoscriptus* became infected and it was hard to induce them to bite. On one occasion, using Huff's method, six *Aedes notoscriptus* failed to feed on a bird within an hour. Immediately afterwards they were given the opportunity of feeding on man under exactly the same conditions. Four of the six fed within half an hour. Possibly they do not normally bite birds.

None of the anophelines would feed on the birds although sixteen different attempts were made under varying conditions as follows. The mosquitoes were kept without food and water for periods up to 48 hours and were, at times, cooled to 4° C. or warmed to 37° C. just before the attempted feeding; the feeding cage was kept either at room temperature, which ranged from 13°-20° C., or put in the incubator at 23°-25° C.; sometimes the humidity was increased by placing a wet towel over the cage. On one occasion eight anophelines that had failed to feed on a bird overnight were given the opportunity to feed on man. Two fed within one hour. Although these experiments took place under highly artificial conditions, they suggest the possibility that *Anopheles annulipes* does not normally bite birds.

In this work very few birds other than sparrows have been examined, but earlier workers, in particular Johnston and Cleland, have examined many species of native birds



from the vicinity of Sydney for plasmodia without finding any infected. So, although the local sparrows in Sydney are heavily infected, their infection does not seem to have been transmitted to the indigenous species of birds. It may be remarked in passing that it proved impossible to infect a zebra finch (*Taeniopygia castanotis* Gould) by inoculation of blood from a sparrow infected with *P. relictum*.

## SUMMARY.

(1). Of 100 birds examined for blood protozoa 66 were positive for *Plasmodium*, 27 for "Toxoplasma" and 1 for *Haemoproteus*.

(2). *Culex fatigans* is an efficient laboratory vector of *P. relictum* and *P. cathemerium*.

(3). It is impossible to distinguish clearly between *P. relictum* and *P. cathemerium* in Sydney sparrows by the usual morphological character applied overseas.

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## STUDIES ON AUSTRALIAN ERYTHRAEIDAE (ACARINA).

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(Twenty-four Text-figures.)

[Read 27th March, 1946.]

### INTRODUCTION.

In 1934 Womersley reviewed the Australian Erythraeidae, describing a number of new adult and larval species, and incorporating the previous work of Rainbow (1906) and Hirst (1926, 1928). He published a further paper in 1936. Since then the Smarididae have been dealt with separately by Womersley and Southcott (1941) and Southcott (1946), and the only paper published on Erythraeidae proper since the two by Womersley has been a short one by Gunther (1941) on a new species of *Balaustium* from New Guinea.

The larvae described by Womersley in 1934 were classified as: *Erythraeus* (3 spp.), *Leptus* (2 spp.), *Hauptmannia* (2 spp.), *Balaustium* (*sic*) *cristatum* and *Bockartia* (*sic*) *? longipes*, all of these being new. They were allotted to these genera following Oudemans' (1912) tentative classification of the larval Erythraeidae. It is now apparently well recognized in Europe that *Bochartia* Oudemans 1910 (with *B. kuyperi* Ouds. 1910 as genotype) is the larva of *Erythraeus* Latreille 1806 (*s.l.*) (see Vitzthum, 1925; Oudemans, 1937, following André, 1929, and Pussard and André, 1929). Womersley's *Bockartia* *? longipes* (corrected to *Bochartia* in 1936) was doubtfully allotted by him to Oudemans' genus. The author has been able to confirm the European correlation of the adult *Erythraeus* with the larval *Bochartia* by (1) proving that *B. longipes* is the larva of *Erythraeus urrbrae* Wom. 1934 (which has page and absolute priority, an *Erythraeus longipes* having previously been described), by the rearing of the larvae, taken parasitic in the field, to the adult, on two occasions, and by a number of lesser rearings; (2) the rearing of larvae from eggs laid by the adults of *Erythraeus reginae* (Hirst 1928) and *E. pilosus* (Hirst 1928) in captivity; (3) the rearing of larvae of *E. reginae*, hatching out from eggs taken in the field, to the nymph (and on one occasion to the adult); (4) rearing a larva of *E. pilosus*, taken parasitic in the field, to a nymph; (5) the rearing of the larva *Erythraeus osmondensis*, n. sp., taken parasitic in the field, to a nymph.

The rearings of the adults (*E. reginae* and *E. urrbrae*) from the larvae are the first ever achieved experimentally in this family.

In 1936 Womersley erected *Bochartia oudemansi* for another new larval species from South Australia. This species comes closer to Oudemans' definition of *Bochartia*. It is in all probability the larva of *Erythraeus imperator* (Hirst 1928), which species Womersley synonymized with *Erythraeus celeripes* (Rainbow 1906), although actually these are two quite distinct species (see further in text).

The discovery of a good deal of new material has necessitated the erecting of three new adult genera for Erythraeidae with 2 eyes on each side, i.e., related to *Erythraeus* Latr. 1806. These are: *Erythrellus*, n. gen., for an aberrant form in which the dorsal setae are modified to an imbricate scaling, with only one species, *Erythrellus imbricatus*, n. gen., n. sp.; *Parerythraeus gregoryi*, n. gen., n. sp., in which there is a row of stout spines along the ventral side of the palp distally and with some of the leg setae modified (one species only); *Erythroides*, n. gen., for forms with some highly modified setae on the legs, related to the last genus, with four species (*Erythraeus serratus* Wom. 1934 the genotype; the other three species are new). The separation of these genera from *Erythraeus s. str.* has been confirmed by the discovery of the larva of *Erythroides*, n. gen.,

which is very distinct from the here recorded larvae of *Erythraeus*. So far these new genera are known only from Australia.

The larval genus *Erythraeus* Oudemans 1912 was a completely incorrect correlation. The definition included "one eye on each side". It is a heterogeneous collection of larvae. In 1936 Womersley erected *Callidosoma* as new for his *Caeculisoma ripicola* Wom. 1934 (adult). A further species of adult *Callidosoma*—*C. womersleyi*, n. sp.—is described in this paper, and has been correlated with its larva by experimental rearings. This larva comes within the definition of *Erythraeus* Oudemans 1912 (*s.l.*), providing further evidence of Oudemans' errors in correlation.

The larval genus *Leptus* Latr. 1796 has previously been correctly correlated with its adult. A confirmation of this has been obtained by the rearing of a larva, from South Australia, to a nymph (not described in this paper).

The larval genus *Hauptmannia* is not considered here, the author having suggested (1946) that it should be referred to the family Smarididae.

Womersley's larval *Balaustium* (*sic*) *cristatum* was referred to that genus following Oudemans' classification. It has been possible to prove that this species is actually a larva of the adult genus *Microsmaris* Hirst 1926. It is quite possible, however, that Oudemans' correlation of his larvae with the adult genus *Balaustium* von Heyden 1826 was correct; *Balaustium* and *Microsmaris* appear to be fairly closely related, and *Microsmaris* has so far been recorded from only Australia and New Zealand.

Much of the work recorded here was done with material from Glen Osmond, near Adelaide, in the Mt. Lofty Ranges, South Australia. Two situations there (and many others to a lesser degree) have been examined frequently from 1936 to 1940, on an average weekly, during that time (and also to a less extent earlier and later). One of these two situations, the richer in species, was a sheltered paddock containing a large red-gum (*Eucalyptus rostrata*) and some red-gum saplings. The predominant winter vegetation here was a heavy growth of *Oxalis cernua* (Soursob), this being replaced toward the summer by *Echium plantagineum* (Salvation Jane) and *Avena fatua* (wild-oat), these being the dominant species (various other herbs are also present). Here the adults of *Erythraeus reginae*, *Erythraeus guttatus*, n. sp., *Erythraeus urbrae*, *Erythroides serratus*, *Erythroides neoserratus*, n. sp., *Leptus* spp., *Microsmaris* sp. (spp.?), etc., occur in the summer, their larvae occurring from up to a few months before (some larvae being tentative); *Erythraeus imperator* adult is found in July–December, with its probable larva, *Erythraeus oudemansi*, occurring in March–May.

The second situation was an exposed hillside, with a row of sugar-gums (*Eucalyptus cladocalyx*) running across its foot. Here there was only slight ground vegetation, both in winter and summer, and a smaller amount of leaf and bark debris around the bases of the trees. From this situation *Erythraeus imperator* and *Erythraeus oudemansi* were absent; and the adults *Erythraeus reginae*, *Erythraeus urbrae*, *Erythroides serratus* and *Erythroides neoserratus*, n. sp. occurred in smaller numbers. *Microsmaris*, both adult and larval, was quite common. Here also *Erythrellus imbricatus*, n. gen., n. sp., was found; it has not been found in other situations.

#### BIOLOGY.

The larvae of the Erythraeidae are parasitic on insects and arachnids; unlike the related Trombidiidae, none are known to attack vertebrates (some Trombidiidae parasitize insects, however). These complete rearings and partial rearings listed above enable the life-history of the Erythraeidae to be defined:

Eggs are laid by the adult females, and hatch to six-legged larvae in from 5–11 months. The larvae run about actively in grass, up tree trunks and in foliage, and will live up to 3 weeks without food. They find a suitable insect or arachnid host (most species show marked preferences), attach by their mouth-parts, and immediately extend their legs straight backwards alongside the body (presumably to raise the body fluid pressure and thus aid in the insertion of the chelicerae). After from a few minutes to half an hour, the legs relax, and now become flexed around the posterior pole of the animal, and remain thus, taking no part in the attachment (this position of the legs renders the larvae, which are frequently on exposed positions of the host, less likely

to be dislodged by being knocked against vegetation, etc.). After some days of feeding the larva is fully-fed, having increased considerably in size, e.g., from  $350\mu$  body length to  $900\mu$ ; under experimental conditions, if the larva is dislodged before it is fully-fed, it will generally re-attach itself to a fresh host (though it may now be less active). After becoming fully-fed it drops off the host. If the host is killed the larva frequently does not detach itself; particularly is this so with the thicker-skinned insects and arachnids, and experimentally it is necessary, in order to ensure its survival, unless it is fully-fed and has thus stopped sucking the fluids of the host, to detach the larva with a brush before the putrefaction of the host. After dropping off the host, the larva may wander around the tube for several days, eventually becoming immobile. After a day or more in this state the red coloration leaves the legs, and the skin splits transversely around the body, just behind the scutum dorsally, and between coxae II and III ventrally, revealing a hairy post-larval pupa (pupa I). The two pieces of the larval skin remain attached to the anterior and posterior poles of the pupa. The anterior piece comprises the larval capitulum, dorsal scutum and legs I and II, and is generally fairly firmly attached; the posterior piece consists of the skin of the dorsum behind the scutum (with the eyes in the genus *Callidosoma* at least) and the skin of the posterior pole of the larva, including legs III, and is usually loosely attached. The pupa I stage lasts 9-16 days; then the nymph emerges. This has an anus, but the genitalia are immature (the larva has neither genitalia nor anus). The nymph feeds on small insects for several weeks, the nymphal stage lasting (experimentally) 21-39 days. The nymph becomes immobile over the last few days, the skin then splits transversely, revealing pupa II. This stage lasts 15-16 days, and then the adult male or female emerges.

#### EXPERIMENTAL METHODS.

Despite the complexity of the life-history, it has been possible to rear several species of *Erythraeus* to nymphs, and two species on to adults; rearings of *Erythroides*, *Leptus* (not described in this paper), *Callidosoma* and *Microsmaris* have been achieved with larvae taken free or parasitic in the field; or, in the case of *Erythraeus* only, with larvae hatching from eggs taken in the field some months before hatching.

Many adult Erythraeidae, e.g., *Erythraeus*, *Erythroides*, *Balaustium* and *Microsmaris* will lay eggs in captivity, but so far only the larvae of *Erythraeus reginæ* (Hirst 1928) and *Erythraeus pilosus* (Hirst 1928) have hatched out from eggs thus obtained. Two quite common larvae at Glen Osmond, South Australia, and elsewhere—*Erythraeus oudemansi* (Wom. 1936) and *Microsmaris* sp.—have never been observed parasitic on insects in the field by the author, nor has any insect offered ever been parasitized, and attempts at rearing these through to nymphs necessitate the selection of the largest specimens in the field; by this means a nymph was obtained from a larval *Microsmaris* (thus showing that Womersley's *Belaustium cristatum* (larval) belongs to *Microsmaris*); attempts at rearing *E. oudemansi* to the nymphal stage have not been successful, as it has not been possible to obtain an engorged larva of this species since the adoption of the above-mentioned methods.

The nymphs obtained from larvae or eggs taken in the field are not sufficient for correlations with adults from the same situation in all cases, although this can sometimes be done. They can always be used, however, for the correlation of previously uncorrelated adult and larval genera; the nymphs of *Erythraeus osmondensis*, n. sp. (larval), *Erythroides clavatus*, n. sp. (larval), and *Microsmaris* obtained from these sources enabled these larvae to be correlated correctly with their adult genera. Pupae are occasionally taken in the field, in soil and leaf débris, sometimes with the skins of the preceding stage attached (and with pupae I can then be used in the correlation of larvae with nymphs and therefore possibly with adults).

Since this work was started in 1936, various species of insects have been used as hosts, e.g., jassids (Homoptera) from eucalypt foliage, Psocoptera, etc. It has been found that, with the majority of the larvae of *Erythraeus* at least, as good or better results can be obtained by keeping them in tubes with adults (and sometimes nymphs) of a common small yellow jassid as host; these jassids can be obtained in large numbers by sweeping a couch-grass (*Cynodon dactylon*) lawn in Adelaide, during the summer

months, when the majority of the larval erythraeids occur. These hosts live for several days, and are removed as soon as they are dead, and fresh ones introduced; the larvae re-attach (it may be necessary to help them on with a fine brush). These jassids are also used to feed the nymphs and adults (some are given squashed, to make the body fluids more accessible). The jassids live longest when a small piece of fresh green grass, about 1 cm. long, is put in the tube, on which they feed and rest. The humidity within the tube is controlled by placing droplets of water on the inside of the cork. Some species, however, show marked host preferences in the field at least, e.g., for thrips, or Psocoptera, e.g., *Troctes divinatorius* L., and various insects and arachnids (e.g., chelifers) may have to be tried. The corks of the tubes must be well-fitting and free from cracks, and the author makes it a practice to slice them cleanly with a razor before each experiment, as otherwise the larvae will hide in the cracks or become squashed between the cork and the glass. The use of cotton-wool plugs is unsatisfactory, as the humidity is then difficult to control, and also the mites burrow into the cotton-wool and become entangled and damaged.

It is possible to determine the species of a larva while still alive, and thus to select species that have not previously been bred. A small ( $\frac{3}{4}$  inch) cover-glass is lowered gently on the larva, which can then be submitted to the high power of the microscope with safety; the larvae can be determined from the keys given in this paper. The larval (and pupal) skins left when the nymph emerges are mounted, and used to check the previous specific determination, although it is not now possible to check the number of the eyes (which must be recorded beforehand); the arrangement of the dorsal setae is also no longer available but this is not a key character. However, unlike some of the Trombidiidae, the number of the eyes is the same in the larvae, nymphs and adults in all the species known to me, and this frequently enables one to make tentative correlations. In addition, in the field, one can frequently make tentative correlations from the times of appearance of the various stages, and the relative numbers of the larval and adult species, e.g., *Microsmaris*. It is also often possible to separate the larval species free in the field by slight differences in colour and rate of progression; these selected larvae are then submitted to the high power of the microscope. Larvae taken parasitic in the field are best not examined with the high power until they detach themselves from the host.

All the figures in this paper were drawn with the aid of a *camera lucida*, the drawings of all the pupae and most of the nymphs being made from the living material. To do this the pupa, or nymph, is placed in a well-slide, and protected by a cover-glass from currents of air (a drop of water from a brush will cause the cover-glass to adhere sufficiently firmly). The nymph can be drawn in the immobile stage prior to ecdysis to pupa II. The specimens require no damage if carefully handled and not submitted to too intense illumination. Wherever possible the type material has been used in the descriptions and illustrations. (This is indicated in the text and descriptions of figures.)

In the descriptions, the body lengths are given to the anterior end of the crista in the adult, and to the anterior end of the dorsal scutum in the larva. The leg measurements include the coxae and claws, except in one instance (recorded in the text); the tarsal lengths given are exclusive of the claws.

#### REMARKS ON TAXONOMY.

With the wealth of material that has been obtained at Glen Osmond, plus the collecting that has been done over many parts of Australia, it has been possible to revise the taxonomy of only part of the family, and it has not even been possible to work out completely the taxonomy of the genera considered here. In fact, such may have to wait until the larvae of many of them are known; as in Trombidiidae, the larvae frequently show greater divergences than the adults. The taxonomic revision covered in this paper is set out in the summary at the end.

#### *Key to the Genera of Australian Adult Erythraeidae with Eyes Two on Each Side.*

- A. Dorsal setae modified to an imbricate scaling ..... *Erythrellus*, n. gen.  
Genotype, *Erythrellus imbricatus*, n. sp.

AA. Dorsal setae not modified so.

B. With some highly modified serrate setae on the legs.

C. With a row of stout conical spines on the ventral side of the palpal tibia distally, and some similarly placed on the palpal genu. Serrate setae of legs asymmetrical . . . . . *Parerythraeus*, n. gen.

Genotype, *Parerythraeus gregoryi*, n. sp.

CC. Without these conical spines on the palpi. Serrate setae of legs symmetrical . . . . . *Erythroides*, n. gen.

Genotype, *Erythraeus serratus* Womersley 1936.

BB. Without serrate setae on the legs . . . . . *Erythraeus* Latreille 1806

Genotype, *Acarus phalangoides* de Geer 1778.

### Genus ERYTHRELLUS, n. gen.

*Definition*: Erythraeidae with eyes two on each side, and with the dorsal body setae modified to an imbricate scaling.

*Genotype*: *Erythrellus imbricatus*, n. sp.

Larva not known.

### ERYTHRELLUS IMBRICATUS, n. sp. Fig. 1, A-H.

*Description of Adult (Type)*: Black dorsally, reddish ventrally on body, and on legs. Body as figured, 1050 $\mu$  long by 740 $\mu$  wide. Crista present, linear, covered over by the imbricate scaling except at the anterior and posterior sensillary areas; distance between

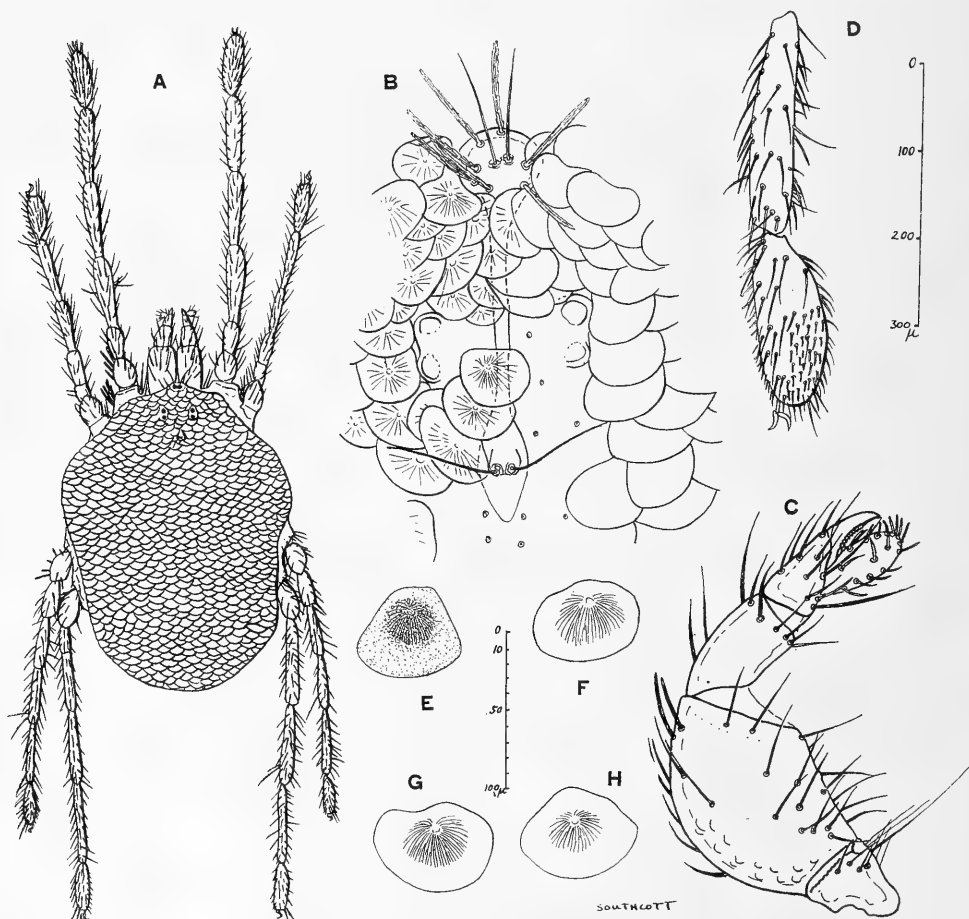


Fig. 1.—*Erythrellus imbricatus*, n. gen., n. sp. A, Dorsal view, entire; B, Anterior region of dorsum, specimen with some scales removed, showing crista and eyes; C, Palp; D, Tarsus I and metatarsus I; E-H, Dorsal setae (pigmentation shown in E only), all to scale shown.

centres of anterior and posterior sensillae  $270\mu$ . Crista continues slightly beyond the posterior sensillary area. Sensillary setae comparatively stout, tapering, pointed, with faint adpressed ciliations, anterior  $104\mu$  long, posterior  $104\mu$  long (in one of the three specimens the posterior sensillary area is completely absent, the crista ending blindly just behind the eyes, and the region where the posterior sensillary area would be expected is covered completely by the typical imbricate scaling). Anterior sensillary area in addition with 6-7 stout, slightly ciliated setae, to  $83\mu$  long. Eyes 2 + 2, behind middle of crista. Dorsal setae highly modified to an imbricate scaling. The scales arise from pedicels which attach excentrally to their under surfaces. On the under surface of the seta, centering on the pedicel, is a fan of striations (see Fig. 1, E-H). The scales are pigmented, and somewhat irregular and variable in shape,  $60-80\mu$  across by  $50-60\mu$  long. Palpi as figured; palpal setae with adpressed ciliations or almost simple. Claw of palpal tibia strong, its ventral edge irregular. Ventral surface of body encroached on only slightly by the scaling, except posteriorly, where the scales extend as far forward as the anus; otherwise venter with spiniform setae with very faint adpressed ciliations, to  $80\mu$  long. Legs with normal setae: leg I  $1620\mu$  long, II  $1230\mu$ , III  $1320\mu$ , IV  $1900\mu$  (all including coxae and claws). Tarsus I  $240\mu$  long by  $75\mu$  high; metatarsus I  $300\mu$  long.

*Localities*: Glen Osmond, South Australia, 3 specimens from débris of leaves and bark at the foot of *Eucalyptus cladocalyx*, 8th Jan., 1939 (1 specimen), 15th Jan., 1939 (1 specimen, type), 16th Jan., 1941 (1); all in author's collection. (All specimens used in the figures.)

*Remarks*: A rare species, only 3 having been found despite regular searching. Each of the 3 specimens was kept alive in a tube for about 3 weeks, but no eggs were laid. Immature eggs about  $300\mu$  long by  $250\mu$  across were present within the adults. At least 2 of the 3 were females, including the type.

#### Genus PARERYTHRAEUS, n. gen.

*Definition*: Eyes two on each side. With highly modified asymmetrically serrate setae on the legs. With a row of stout conical spines on the ventral (flexor) side of the palpal tibia distally, and some similarly placed on the palpal genu. Palpal claw with a single blunt basal tooth.

*Genotype*: *Parerythraeus gregoryi*, n. sp.

Larva not known.

#### PARERYTHRAEUS GREGORYI, n. sp. Fig. 2, A-I.

*Description of Adult (Type)*: Red, very large mite. Body oval, length 2.7 mm., width 1.9 mm. Crista linear,  $695\mu$  between centres of anterior and posterior sensillae. Sensillary setae fine, tapering, simple, anterior  $157\mu$  long, posterior  $190\mu$ . Anterior sensillary area also with 10 long non-sensillary setae, some slightly clavate, with ciliations modified to serrations, to  $275\mu$  long. Eyes 2 + 2, behind middle of crista. Dorsal setae pigmented, clavate, dorsally convex with rows of adnate serrations, ventrally with a small ciliated keel, and rows of fine ciliations alongside; dorsal setae  $40-50\mu$  long. Ventral setae not modified, pigmented, tapering, ciliated, to  $80\mu$  long, but longer and thicker over coxae. Palpi as figured, with a row of 7 conical spines along the ventral (flexor) edge of the palpal tibia distally, and 3 more similarly placed distally on the palpal genu. These conical spines are pigmented, roughened ventrally, smooth dorsally (see figure). Setae of palp (except tarsus) somewhat ciliated. Tibial claw smooth except for one broad blunt basal tooth. Legs long: I 6.2 mm., II 4.2 mm., III 5.0 mm., IV 8.8 mm. (all including coxae and claws). Tarsus I  $680\mu$  long by  $235\mu$  high; metatarsus I  $1520\mu$  long. Clothing of legs almost entirely of the asymmetrically serrate setae down to middle of tibiae; a number of these setae are present on the proximal half of the metatarsi dorsally; otherwise tibiae, metatarsi, and tarsi entirely with normal ciliated setae, and a few of these setae on the more proximal segments. Fine spiniform sensory setae are also present on the legs.

*Locality*: Coomalie Creek, Northern Territory, 20th May, 1943, in leaf débris, one specimen, type (R.V.S.); in author's collection.

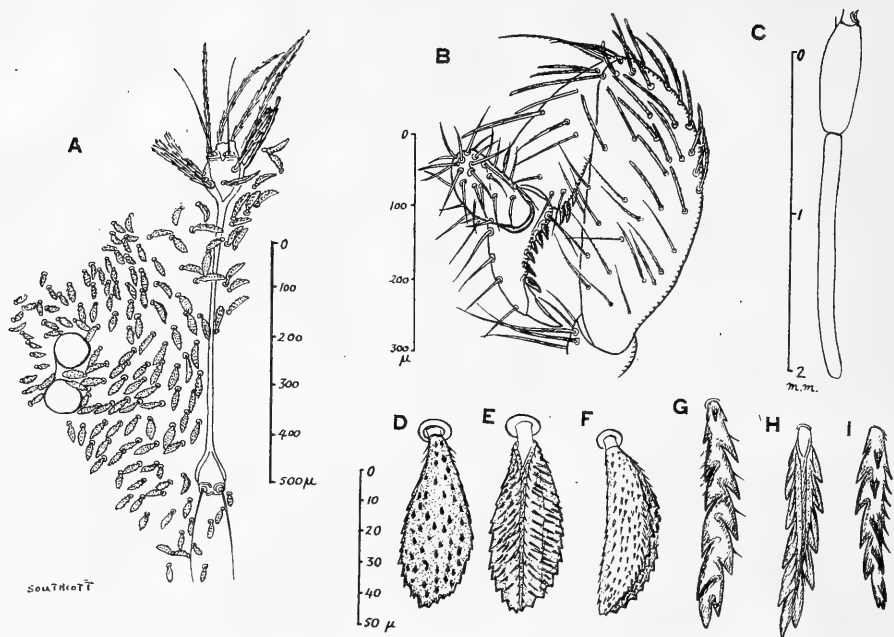


Fig. 2.—*Parythraeus gregoryi*, n. gen., n. sp. A, Anterior region of dorsum, showing crista and eyes; B, Palp; C, Tarsus I and metatarsus I, outline; D-I, Setae, all to scale shown; D, Dorsal seta from above; E, Same from below; F, Same, side view; G, H, I, Serrate setae from legs, from above, below, side. (All figures from the type.)

Genus ERYTHROIDES, n. gen.

*Definition*: Eyes two on each side, on distinct shields. With highly modified symmetrically serrate setae on the legs. No spines to the ventral edge of palp. Palpal claw with fine teeth basally. Narrow shield to crista present.

*Genotype*: *Erythraeus serratus* Womersley 1936.

Larva with two eyes on each side. Dorsal scutum somewhat pentagonal, with 3 pairs of non-sensillary setae, and 2 pairs of clavate sensillary setae. One seta to each trochanter. Ventral surface of body with a pair of setae between or just behind the inner angles of coxae I, and one pair of setae between the levels of coxae II and III. Palpal claw with a dorsal tooth. Each coxa with one seta.

Larva known from only *Erythroides clavatus*, n. sp.

Key to the Adult Species of Erythroides, n. gen.

- A. Dorsal setae convex, considerably expanded, leaf-like.
  - B. Dorsal setae triangular, with blunt serrations . . . *Erythroides serratus* (Wom. 1936)
  - BB. Dorsal setae elongate-oval, with numerous fine serrations . . . . . *Erythroides neoserratus*, n. sp.
- AA. Dorsal setae elongate, not or only slightly expanded distally.
  - C. Dorsal setae widest distally (i.e., slightly clavate), heavily pigmented. Cilia-tions absent from proximal part of seta. Serrate setae numerous on metatarsi . . . . . *Erythroides darwini*, n. sp.
  - CC. Dorsal setae somewhat lanceolate, lightly pigmented; serrations present along whole length of seta. Only a few serrate setae present on metatarsi . . . . . *Erythroides macdonnelli*, n. sp.

ERYTHROIDES SERRATUS (Womersley 1936). Fig. 3, A-D.

*Erythraeus serratus* Womersley 1936, *J. Linn. Soc. Lond., Zool.*, 40(269) : 117.

The type adult (male) was described and figured by Womersley, drawings of the front tarsus and metatarsus being included. The palpi also were figured, the tibial claw being shown as simple. Actually there are fine basal serrations to the tibial claw. The dorsal setae and palp are re-figured here, and the following additional details (from the



type ♂) given: Sensillary setae tapering, with fine adpressed ciliations, posterior sensillary setae  $105\mu$  long. Dorsal setae heavily pigmented, triangular, with heavy serrations,  $24-32\mu$  long; a few of these setae, where the dorsal vestiture is continued over on to the ventral surface posteriorly, near the anus, are unpigmented. The serrate setae of the legs extend over the trochanters to the metatarsi, mingled with the ordinary ciliated leg setae, and more on the extensor side. The serrate setae are not present on the tarsi.

*Localities:* The type ♂ was from Bathurst, New South Wales, 31st May, 1934. This species is found at Glen Osmond, South Australia, in bark and leaf débris at the bases of eucalypts, etc., along with *Erythroides neoserratus*, n. sp. Adults of both species occur during August to January (commonest in November-January), though occasional specimens of *Erythroïdes serratus* have been taken in May and July (survey over 1936-1940).

*Remarks:* See under the remarks for *Erythroïdes neoserratus*, n. sp., and for the larval *Erythroïdes clavatus*, n. sp.

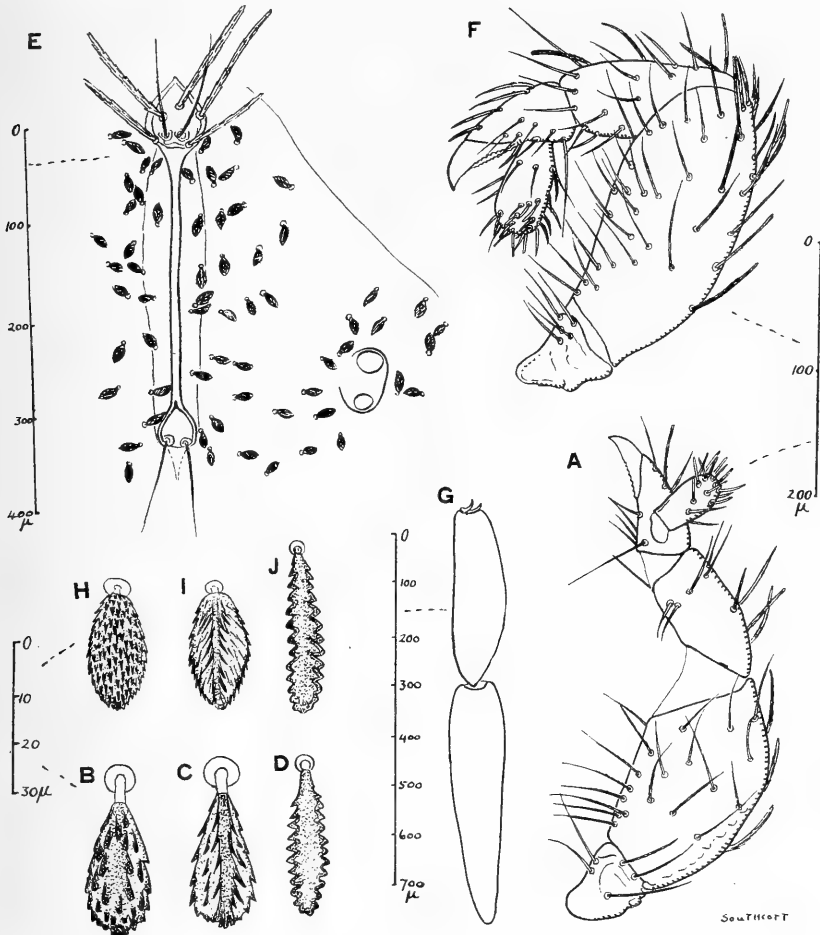


Fig. 3.—A-D, *Erythroïdes serratus* (Wom. 1936). A, Palp; B, Dorsal seta from above; C, same from below; D, Serrate seta from legs. E-J, *Erythroïdes neoserratus*, n. sp. E, Anterior region of dorsum; F, Palp; G, Tarsus I and metatarsus I; H, Dorsal seta from above; I, Same from below; J, Serrate seta from leg. (All setae to scale shown; all figures from types.)

ERYTHROIDES NEOSERRATUS, n. sp. Fig. 3, E-J.

*Description of Adult (Type ♂):* Reddish, with white bandings on the hind legs. Body length 1.4 mm., width 1.0 mm. Crista linear, with shield as figured, and the normal

two sensillary areas. Distance between centres of anterior and posterior sensillae  $320\mu$ . Sensillary setae tapering, with fine adpressed ciliations, anterior sensillary setae  $104\mu$  long, posterior  $105\mu$ . Eyes 2 + 2, on distinct shields, behind middle of crista. Dorsal setae heavily pigmented, elongate-oval (not triangular), with numerous fine-pointed ciliations as figured, setae  $16-28\mu$  long. Ventral setae tapering, with adpressed ciliations, to  $70\mu$  long. Palpi as figured, palpal claw basally with fine teeth. Legs long, heavily setose, with white bandings on legs IV: I  $2400\mu$  long, II  $1850\mu$ , III  $2500\mu$ , IV  $4050\mu$  (all including coxae and claws). Tarsus I  $480\mu$  long by  $102\mu$  high, metatarsus I  $500\mu$  long, tarsus IV  $320\mu$  long, metatarsus IV  $1170\mu$  long. All tarsi with scopulae. The serrate setae of the legs are mingled with the normal ciliated setae from trochanters to metatarsi, these serrate setae being mainly on the extensor side; only a few serrate setae are present on the metatarsi, and these proximally; none on tarsi. Numerous short simple curved sensory setae are also present on the legs. On the distal portion of genu IV and tibia IV the setae are unpigmented, including some serrate setae, giving white bandings, by which this species is easily distinguished from the preceding, macroscopically.

*Localities:* Present along with the preceding species at Glen Osmond, South Australia, in bark and leaf debris, during the summer months; it is commoner than *Erythroides serratus*. See remarks for *Erythroides serratus*, and for *Erythroides clavatus*, n. sp. (larval).

Type ♂ from Glen Osmond, 26th Nov., 1939; in author's collection.

ERYTHROIDES CLAVATUS, n. sp. Figs. 4, A-K; 5, A-C.

*Description of Larva (Type).* Fig. 4, A-H: Red. Body ovoid, length  $395\mu$ , width  $240\mu$ . Dorsal scutum pentagonal, with rounded angles,  $106\mu$  long by  $132\mu$  wide. Anterior and posterolateral borders of shield are very slightly concave, anterolateral borders are very slightly convex. Shield with 2 pairs of ciliated clavate sensillary setae, anterior  $31\mu$  long, posterior  $40\mu$ ; also with 3 pairs of non-sensillary setae, stout, clavate, ciliated, the anterior 2 are near the anterolateral angles of the shield, length  $59\mu$ , the middle 2 are level with the anterior sensillae,  $47\mu$  long, the posterior 2 are stronger than the other 4, arise at the level of the middle of the shield and are  $58\mu$  long. Eyes 2 + 2, each lateral pair on a distinct shield. Dorsum with about 43 stout clavate ciliated setae,  $46-52\mu$  long, arranged 2, 4, 8, 4, 5, 8, 7, 5; the ciliations are strong, tapering and somewhat blunted (blunted more on the setae distally). Venter: between coxae I 2 setae, simple, pointed,  $50\mu$  long; between the levels of coxae II and III a similar pair  $44\mu$  long; well behind coxae III is a transverse row of 4 clavate ciliated setae  $37-39\mu$  long; arranged around the periphery of the posterior pole of the body ventrally are about 10 ciliated clavate setae  $40-41\mu$  long. Seta on coxa I arises at its posterolateral angle, curved, pointed, ciliated,  $94\mu$  long; seta on coxa II arises near its posterolateral angle, straight, blunt, ciliated,  $42\mu$  long; that on III arises near the centre of the coxa, slightly curved, blunt, ciliated,  $50\mu$  long. Legs long and thin: I  $772\mu$  long, II  $777\mu$ , III  $960\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $125\mu$  long by  $28\mu$  high; empodium strong, falciform, ridged; anterior claw with a straight shaft and terminal hook, the shaft with many ventral ciliations, and with 8 teeth or adpressed ciliations along its dorsal edge; posterior claw retroflexed and with many branching ventral ciliations. Almost all the setae of the tarsus are curved, long, strongly ciliated. Metatarsus I  $186\mu$  long. Capitulum as figured. The posterior pair of hypostomal setae are ciliated. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 7 setae respectively. Palpal claw with a dorsal tooth. Palpal tarsus as figured.

*Description of Post-Larval Pupa (Pupa I).* (ACA 360). Figs. 4, I-K; 5, A, B: Red. Length  $600\mu$ , width  $350\mu$ . Shape ovoid, evenly rounded posteriorly, rather pointed anteriorly, and there notched, ventral surface flattened. With a number of fairly strong, slightly tapering, blunted, slightly curved setae, with adpressed ciliations nearer the proximal end of the seta, and with freer ciliations distally; each seta arising from a papilla; setae  $22-62\mu$  long.

*Description of Nymph.* (ACA 1013). Fig. 5, C: Red. Body  $540\mu$  long,  $410\mu$  wide. Crista normal; sensillary setae tapering, with fine adpressed ciliations, anterior sensillary

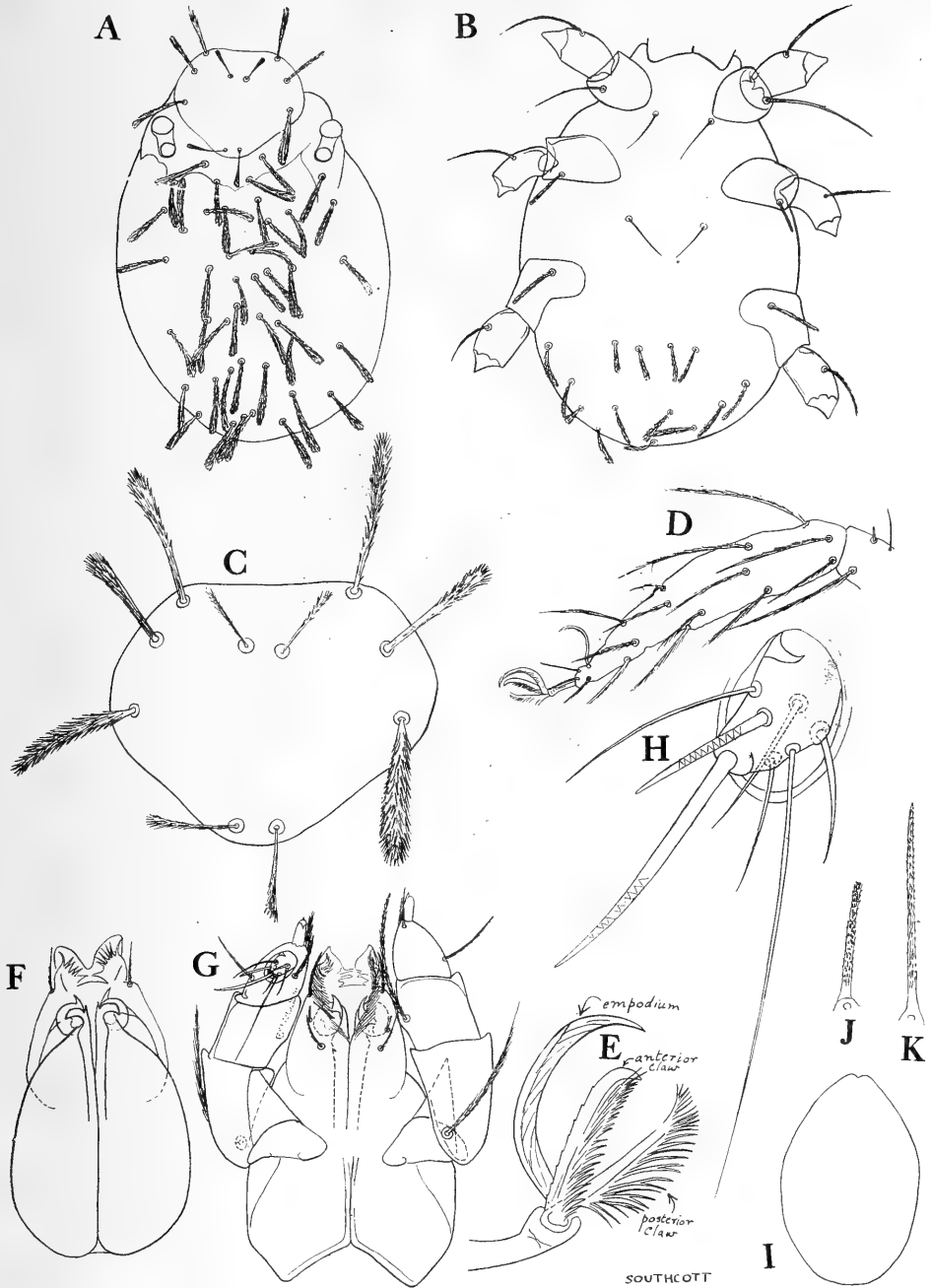


Fig. 4.—*Erythroides clavatus*, n. sp. A-H, Larva. A, Dorsum; B, Venter; C, Dorsal scutum; D, Tarsus I; E, Tip of tarsus I; F, Capitulum from above; G, Same from below (with dorsal view of palp on right); H, Palpal tarsus; I-K, Post-larval pupa (pupa I). I, Outline; J, K, Setae. (Figures A-H from type larva, I-K from ACA 360; see text.)

setae  $90\mu$  long, posterior  $96\mu$  long. Distance between centres of anterior and posterior sensillae  $204\mu$ . Eyes  $2+2$ , each lateral pair on a distinct shield. Palpal claw basally with fine teeth. Dorsal setae as in Fig. 5, C, pigmented, with blunted serrations,  $14-18\mu$  long, some longer near the nasus to  $28\mu$ . Distribution of serrate setae on the legs as for

*Erythroides serratus* and *Erythroides neoserratus*, n. sp., some being unpigmented on legs III and IV. Legs long: I 1450 $\mu$  long, II 1050 $\mu$ , III 1350 $\mu$ , IV 2700 $\mu$  (all including coxae and claws). Tarsus I and metatarsus I not available for measurement. Tarsus IV 182 $\mu$  long.

*Localities*: All specimens so far have been taken at Glen Osmond, South Australia, in soil and leaf débris at the base, or on the trunk or under bark, of *Eucalyptus rostrata*: 11th Nov., 1937 (1 specimen), 21st Dec., 1937 (2 specimens, one the type), 26th Nov., 1939 (1 specimen, ACA 360, see below), 9th Nov., 1941 (3 specimens, ACA 1012, 1013, 1014, see below); also 2 specimens, Sept.–Nov., 1937 (see ACA 212, below).

*Biology.*

1. Tube ACA 212. An adult *Erythraeus urrbrae* was taken at Glen Osmond on 1st Aug., 1937, and put in a tube with some unsterile soil from the same situation (base of *Eucalyptus rostrata*). On 14th Aug., 1937, the soil was replaced with soil from the same situation; no eggs were seen. On 22nd Aug., 1937, a batch of eggs was seen in the

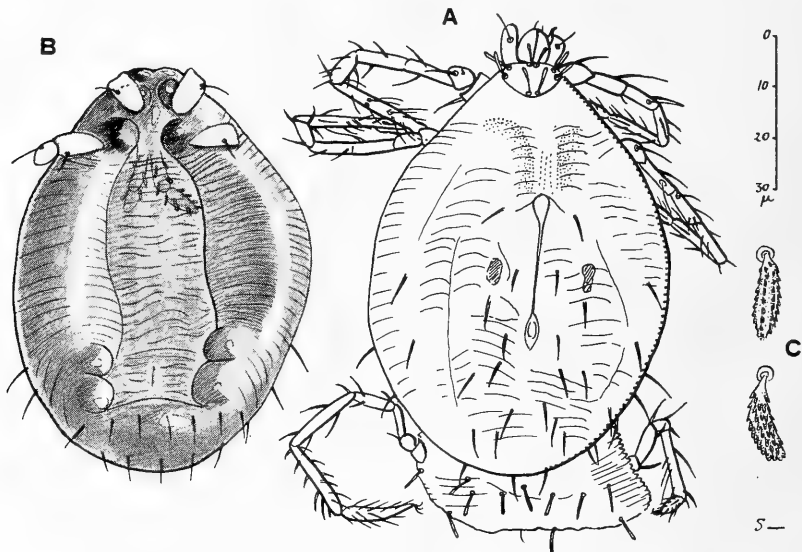


Fig. 5.—*Erythroides clavatus*, n. sp. A, Post-larval pupa (pupa I) with cast larval skin still attached; B, Same from below; C, Nymph, dorsal setae (to scale above) (all figures from ACA 1013; see text).

tube; these were unhatched on 11th Sept., 1937, and the adult *Erythraeus urrbrae* was dead. On 13th Nov., 1937, the tube was emptied out and the contents examined carefully: the dead adult *Erythraeus urrbrae*, 2 dead *Erythroides clavatus*, n. sp. (larval), 28 dead *Leptus anomalus*, n. sp. (larval), and 20 unhatched eggs were found. Nine eggs were mounted and 11 were kept, but no further eggs hatched out. Unsterile soil was used on the assumption that it would provide food for the adult. Elsewhere in this paper the larva of *Erythraeus urrbrae* is described, and also the nymph of *Erythroides clavatus*, n. sp. The adult of *Leptus anomalus*, n. sp. is not known. Presumably the second lot of soil added to the tube contained a mixed batch of eggs; no other mites were found at the final examination.

2. Larva ACA 360, from Glen Osmond, 26th Nov., 1939, was plump, body length 570 $\mu$ , width 340 $\mu$ . It became immobile on 27th Nov., 1939; the larval skin split off on 4th Dec., 1939, revealing pupa I, which was unfortunately damaged (and killed) a few days later.

3. Three larval specimens were taken free on 9th Nov., 1941. ACA 1012 and ACA 1014 lived for a few days only, although jassids were provided as hosts. ACA 1013 was plump when taken, body length 720 $\mu$ , width 490 $\mu$  (i.e., partly fed at least). Several small yellow

jassids were given to act as hosts, and water also. The mite did not attach to any and became immobile on 11th Nov., 1941. It cast its skin on 14th Nov., 1941, revealing pupa I, which was drawn with the aid of a *camera lucida* (Fig. 5, A, B) on 23rd Nov., 1941; length 700 $\mu$ , width 510 $\mu$ . The nymph (described above) hatched out on 26th Nov., 1941. It was given food (insects) and water, but died on 3rd Dec., 1941. Thus the pupa I stage lasted 12 days.

*Remarks:* I am not prepared to correlate specifically the nymph obtained (ACA 1013) with either of the two adult *Erythroides*—*E. serratus* and *E. neoserratus*, n. sp.—occurring at the same situation. The nymphal dorsal setae are not sufficiently like those of either of these two species for a correlation to be proposed.

The scutal setae of the larvae are subject to some variation, e.g., one or both of the anterior sensillary setae or one of the posterior sensillary setae may be only very slightly clavate; hence no great reliance can be placed on this variation as a specific character. Despite the fact that nine larval specimens have been obtained, it has not been possible to separate out another species, though two adult species occurred in fair numbers in the same situation. Further work there later may reveal a second species.

At present, therefore, this larva must be given a separate specific name. The distinct character of the scutal sensillary setae being clavate, plus the pentagonal shape of the scutum, confirms the separation of *Erythroides*, n. gen., from *Erythraeus* s. str.

(All specimens in author's collection.)

#### ERYTHROIDES DARWINI, n. sp. Fig. 6, A–G.

*Description of Adult (Type):* Red. Body oval, length 1.5 mm., width 1.1 mm. Crista linear, with shield as figured. Two sensillary areas to crista, each with 2 sensillary setae with fine adpressed ciliations; anterior sensillary setae 125 $\mu$  long, posterior 127 $\mu$  long. Distance between centres of anterior and posterior sensillae 325 $\mu$ . Anterior sensillary area also with some long strong ciliated setae as figured. Eyes 2+2, each lateral pair on a distinct shield. Dorsal setae elongate, slightly clavate, heavily pigmented, with strong ciliations distally; setae 34–57 $\mu$  long, the more posterior setae the longer. Ventral setae tapering, pointed, finely ciliated, to 90 $\mu$  long. Palp as figured, palpal claw basally with fine teeth. Legs: I 2650 $\mu$  long, II 1950 $\mu$ , III 2400 $\mu$ , IV 4300 $\mu$  (all including coxae and claws). Tarsus I 350 $\mu$  long by 112 $\mu$  high; metatarsus I 540 $\mu$  long; tarsus IV 310 $\mu$  long; metatarsus IV 1450 $\mu$  long. Clothing of legs excluding coxae and tarsi almost entirely of serrate setae; the serrate setae distally on the legs with more and finer serrations than those more proximally placed. Some unpigmented setae present on tibiae IV. The normal (ciliated) leg setae are commoner on the flexor and distal parts of the segments, especially the tibiae, as well as being on the tarsi. No serrate setae on the tarsi. Numerous fine sensory setae are also present on the legs.

*Locality:* A single adult specimen (type) from Adelaide River, Northern Territory, 13th Apr., 1943 (R.V.S.); in author's collection.

*Remarks:* Close to the following species, but differs as indicated in key.

#### ERYTHROIDES MACDONNELLI, n. sp. Fig. 6, H–M.

*Description of Adult (Type):* Red. Body shape normal, length 1050 $\mu$ , width 930 $\mu$ . Crista normal, 285 $\mu$  between centres of anterior and posterior sensillae. Sensillary setae tapering, with fine ciliations, anterior 94 $\mu$  long, posterior 127 $\mu$ . Eyes 2+2, each lateral pair on a distinct shield. Dorsal setae elongate-lanceolate, frequently curved slightly distally, with serrations along the whole length of the seta, setae keeled ventrally, lightly pigmented, 49–68 $\mu$  long. Palp as figured, claw basally with a few very fine teeth. Legs: I 2300 $\mu$  long, II 1350 $\mu$  (approx.), III and IV missing (lengths including coxae and claws). Tarsus I 290 $\mu$  long by 83 $\mu$  high; metatarsus I 510 $\mu$  long. Serrate setae of legs fairly numerous, absent from coxae and tarsi, and only a few present on metatarsi.

*Locality:* One gravid ♀ (type) from Alice Springs, Northern Territory, 21st July, 1942 (R.V.S.); in author's collection.

*Remarks:* Type ♀ contained many spheroidal to ovoid eggs, average size 205 $\mu$  long by 135 $\mu$  across. This species is close to the preceding; distinguished as in key.

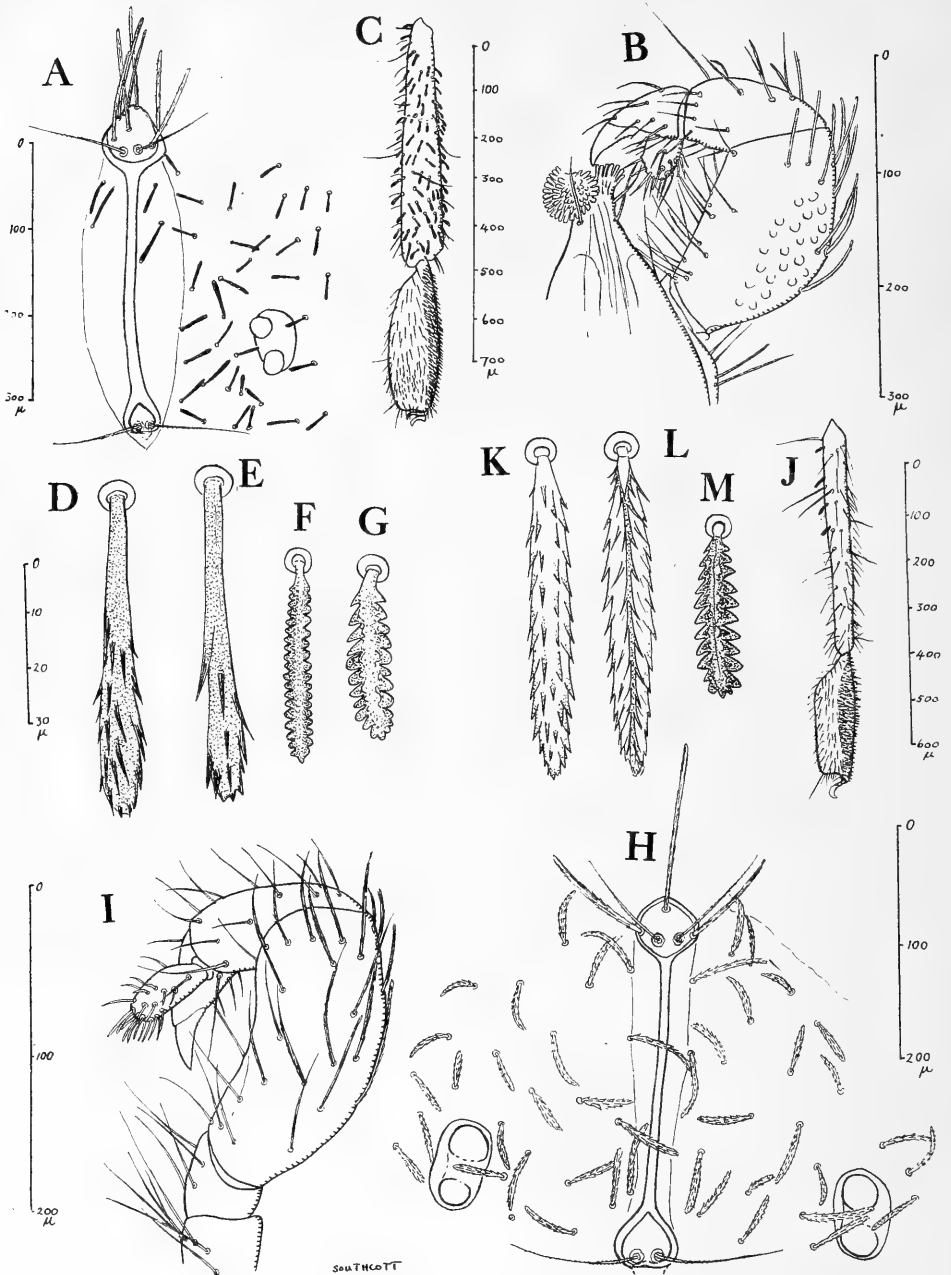


Fig. 6.—A-G, *Erythroides darwini*, n. sp. A, Anterior region of dorsum; B, Mouth-parts and palp from above (fimbriated lip bent back on left); C, Tarsus I and metatarsus I; D, E, Posterior dorsal setae; F, G, Serrate seta from metatarsus I; H-M, *Erythroides macdonnelli*, n. sp. H, Anterior region of dorsum; I, Left palp, lateral aspect; J, Tarsus I and metatarsus I; K, L, Posterior dorsal seta from above; M, Serrate seta from leg. (All setae to the scale shown on the left; all figures from types.)

Genus ERYTHRAEUS Latreille 1806.

*Gen. Crust. Ins.*, 1: 146.

*Bochartia* Oudemans 1910, *Ent. Ber. Amsterdam*, 3: 49; 1912, Womersley 1934, *Rec. S. Aust. Mus.*, 5: 251; 1936.

[non] *Erythraeus* (larval) Oudemans 1912, Womersley 1934.

Prior to the separation of the new genera *Erythrellus*, *Parerythraeus* and *Erythroides* in this paper, *Erythraeus* included all Erythraeidae with two eyes on each side. The adult generic characters of *Erythraeus s. str.* may now be given as: Eyes 2 on each side. Dorsal setae not modified to an imbricate scaling. Palp simple, there being no conical spines distally on its ventral (flexor) side. Without highly modified serrate setae on the legs.

*Re-definition of Larval Characters of Genus Erythraeus:* Eyes 2 on each side. Dorsal scutum generally rounded; flattened or concave anteriorly. Dorsal scutum with 2 pairs of sensillary setae, the anterior pair a little behind the anterior border of the shield, the posterior pair on the posterior border of the shield. Scutum with 2 or 3 pairs of non-sensillary setae, 1 or 2 pairs being placed anteriorly, near the edge of the shield, the hind pair at about the middle of the shield, near the edge. Each coxa with one seta. Legs with 6 segments. Tarsus with a strong falciform empodium and 2 lateral dissimilar modified claws: anterior claw ciliated, with a weak terminal hook, posterior claw retroflexed. Palpal coxa, femur, genu, tibia, tarsus with 0, 1, 1, 3, 7-8 setae respectively.

### Biology.

The larvae attach themselves to any exposed portion of the jassid (Homoptera) or other host, e.g., head or thorax (contrast *Callidosoma* larva).

#### Key to the Australian Adults of Genus *Erythraeus*.

- A. Palpal tibia an equilateral cone. Dorsal setae of male and female dissimilar. Dorsal setae of female in two sizes.
- B. Male dorsal setae fine, spiniform, simple, 30-35 $\mu$  long. Female longer dorsal setae with only a few ciliations, and these at tip.  
Eastern Australia ..... *E. celeripes* (Rainbow 1906)
- BB. Male dorsal setae stouter, strongly ciliated 40-60 $\mu$  long. Female longer dorsal setae with ciliations along their entire length.  
Type locality, Lucindale, South Australia ..... *E. imperator* (Hirst 1923)
- AA. Palpal tibia is generally twice as long as its basal width. Dorsal setae in male and female alike.
- C. Dorsal setae leaf-like.
- D. Without conspicuous white spots on the dorsal surface of the body. Colour red or reddish.  
Type locality, Adelaide, South Australia ..... *E. reginae* (Hirst 1923)  
Type locality, Tanunda, South Australia .....  
..... *E. antepodianus* (Hirst 1923)  
(For further differentiation see in text.)
- DD. With conspicuous white spots on a background of black setae; one large circular white area completely surrounding the posterior sensillary area of the crista.  
Type locality, Glen Osmond, South Australia ..... *E. guttatus*, n. sp.
- CC. Dorsal setae elongate.
- E. Dorsal setae taper to a very fine sharp point, ciliated.  
Type locality, Dubbo, New South Wales. Also found at Glen Osmond, South Australia ..... *E. pilosus* (Hirst 1928)
- EE. Dorsal setae blunted at tip, ciliated.  
Type locality, Adelaide, South Australia .....  
..... *E. urbrae* Womersley 1934

#### Key to the Australian Larvae of Genus *Erythraeus*.

- A. Dorsal scutum with 2 pairs of non-sensillary setae. Each trochanter with 2 setae. Palpal claw trifurcate.  
Type locality, Adelaide, South Australia ..... *E. oudemansi* (Womersley 1936)
- AA. Dorsal scutum with 3 pairs of non-sensillary setae. Each trochanter with one seta. Palpal claw bifurcate.
- B. With 2 pairs of setae on the ventral surface of the body between capitulum and coxae III.
- C. Dorsal setae 30-50 $\mu$  long.
- D. Some or all tarsal setae ciliated.
- E. Ventral setae of tarsus ciliated, dorsal setae of tarsus not ciliated.
- F. Scutum evenly rounded except anteriorly. Dorsal setae not or scarcely expanded distally, with ciliations modified to dagger-like scales, these being blunted distally, more pointed proximally. Anterior sensillary

- setae  $66\mu$  long, posterior  $74\mu$ . Dorsal setae  $35-45\mu$  long.  
 From Glen Osmond, South Australia .....  
 ..... *E. reginae* (Hirst 1928)
- FF. Dorsal scutum squarish, with slightly concave sides behind the middle. Dorsal setae somewhat expanded distally, feather-shaped, ciliations more pointed than in preceding. Anterior sensillary setae  $39\mu$  long, posterior  $54\mu$ . Dorsal setae  $24-34\mu$  long.  
 Type locality, Attack Creek, Northern Territory .....  
 ..... *E. stuarti*, n. sp.
- EE. All tarsal setae ciliated.  
 Type locality, Glen Osmond, South Australia .....  
 ..... *E. osmondensis*, n. sp.
- DD. Tarsal setae not ciliated. Anterior sensillary setae  $94\mu$  long, posterior  $68\mu$ .  
 Larvae from Glen Osmond, South Australia .....  
 ..... *E. pilosus* (Hirst 1928)
- CC. Dorsal setae  $50-85\mu$  long. All setae of tarsus ciliated.  
 Larvae from Adelaide, South Australia ..... *E. womersleyi* Womersley 1934
- BB. With 3 pairs of setae on the ventral surface of the body between capitulum and coxae III. All tarsal setae simple. Dorsal setae to  $50\mu$  long. Anterior sensillary setae  $47\mu$  long; posterior  $61\mu$ .  
 Type locality, Glen Osmond, South Australia ..... *E. womersleyi*, n. sp.

ERYTHRAEUS CELERIPES (Rainbow 1906). Fig. 7, A-C.

*Rhyncholophus celeripes* Rainbow 1906, *Rec. Aust. Mus.*, 6: 156.

*Erythraeus celeripes* Womersley 1934 (part), *Rec. S. Aust. Mus.*, 5 (2): 218.

This species was originally described by Rainbow from Enfield, New South Wales. In 1934 Womersley synonymized Hirst's *Leptus imperator* (1928) from Lucindale, South Australia, with this species, and gave a fresh description with figures, based on Rainbow's material. Hirst's species is, however, quite distinct, as can be seen from the figures of the dorsal setae for the two species (see Fig. 7). Hirst's species is re-described in the following pages as *Erythraeus imperator*. Womersley refers to the dorsal setae of *E. celeripes* as short and spiniform in the text (l.c., p. 219), but in the key (p. 222) records them as long. The confusion was due to the fact that in *E. celeripes* and *E. imperator*, unlike other members of the genus, there are marked differences between the dorsal setae of male and female. Womersley's figure of the short dorsal setae of *E. celeripes* was from the male.

The following additional details of description for the adult *E. celeripes* are given (from Rainbow's type material): Sensillary setae of crista filiform, anterior  $146\mu$  long, posterior  $170\mu$  long. Distance between centres of anterior and posterior sensillae  $670\mu$ . (Crista of this ♂ syntype is  $970\mu$  long; a ♀ syntype  $640\mu$ ,  $920\mu$  respectively.) Dorsal setae of ♂ uniform, short, curved, spiniform (indistinctly ciliated),  $30-35\mu$  long; ♀ dorsal setae in two distinct sizes, longer setae  $160-180\mu$  long, tapering, spiniform, with a few indistinct terminal ciliations, the shorter setae are similar, only indistinctly ciliated, about  $70-90\mu$  long. Palpal tibia, claw and tarsus extremely short. Claw of palpal tibia smooth ventrally except for a basal small single tooth.

*Locality*: Rainbow's material from Enfield, New South Wales "at all seasons of the year".

*Remarks*: See under the following species.

ERYTHRAEUS IMPERATOR (Hirst 1928). Fig. 7, D-F.

*Leptus imperator* Hirst 1928, *Ann. Mag. nat. Hist.*, (10) 1 (4): 570.

*Erythraeus celeripes* Womersley 1934 (part), *Rec. S. Aust. Mus.*, 5 (2): 218.

*Re-description of Adult ♀ (Type)*. Fig. 7, D, E: Red. Body oval, length  $2.5$  mm., width  $1.65$  mm. Crista linear, the anterior sensillary area being produced into a long blunt-pointed nasus carrying many long setae with adpressed ciliations. Length of nasus  $350\mu$ . Sensillary setae of crista long, strong, tapering, only very indistinctly ciliated, anterior  $146\mu$  long, posterior (missing in type)  $200\mu$  long. Crista continues beyond posterior sensillary area. Distance between centres of anterior and posterior sensillae  $900\mu$ . Eyes  $2+2$ , behind middle of crista. Dorsal setae of ♀ in two sizes, the distinction



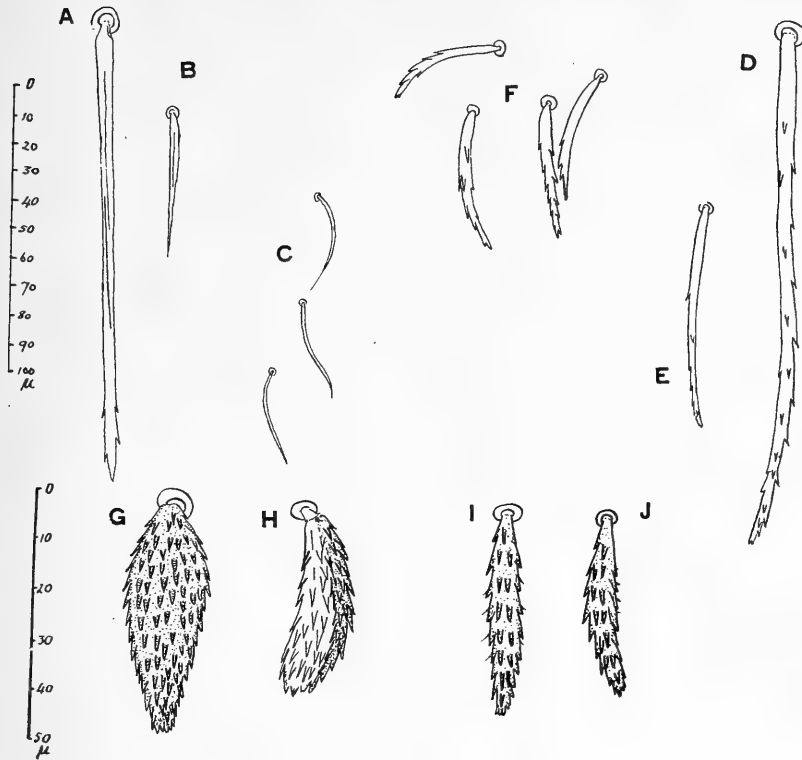


Fig. 7.—A-C, *Erythraeus celeripes* (Rainbow 1906). A, Adult ♀, longer dorsal seta; B, Adult ♀, shorter dorsal seta; C, Adult ♂, group of dorsal setae. D-F, *Erythraeus imperator* (Hirst 1928). D, Adult ♀, longer dorsal seta; E, Adult ♀, shorter dorsal seta; F, Adult ♂, group of dorsal setae. G-J, *Erythraeus reginae* (Hirst 1928). G, Adult, dorsal seta from above; H, Same from side; I, J, Nymph, dorsal setae. (Figs. A-E, G, H, from type material.)

between the two sizes not being as clear as in *E. celeripes*; longer 150–200 $\mu$  long, stout, ciliated along entire length, shorter setae about 80 $\mu$  long, comparatively less ciliated. (Dorsal setae of a ♂ specimen from Glen Osmond, Fig. 7, F, uniform, stout, heavily ciliated, 40–60 $\mu$  long.) Palp similar to that of *E. celeripes*—with a very short tibia, claw, tarsus (which is almost hemispherical); tibial claw smooth, but a blunt protuberance is present basally, ventrally. Legs fairly stout for the genus: I 6.5 mm. long, II 3.9 mm., III 4.6 mm., IV 6.7 mm. (all including coxae and claws). Tarsus I 680 $\mu$  long by 300 $\mu$  high; metatarsus I 1370 $\mu$  long. All tarsi almost oval, and with ventral scopulae.

**Localities:** Type ♀ (Hirst) was from Lucindale, South Australia. The species is not uncommon at Glen Osmond, South Australia, under the bark of eucalypts (*Eucalyptus rostrata* especially) rather than in soil. Nymphs are also obtained by sweeping foliage of *Eucalyptus rostrata*.

#### Biology.

Adults taken at Glen Osmond and elsewhere around Adelaide lay eggs in late October, and November. They are laid in one or two large batches; orange-red when first laid; however, the chorion rapidly blackens. Eggs measure on average 420 $\mu$  long by 300 $\mu$  wide. None of the eggs laid thus have hatched, all either drying out when kept dry, or going mouldy when kept moist. None has progressed to the deutovum stage. The eggs are spheroidal, smooth, polished, but later develop protuberances indicating partial development. Nymphs are found from May to September, under bark and in foliage of *Eucalyptus rostrata*. Adults begin to appear in July (rare), with greatest numbers in October–November, and have disappeared by mid-December.

*Remarks:* The larva is unproven, but is in all probability *Erythraeus oudemansi* (Wom. 1936) (larval) (q.v., remarks).

*Erythraeus celeripes* and *E. imperator* are very distinct from the other Australian members of the genus, as at present constituted, in the great shortening of the terminal segments—tibia and tarsus—of the palp, also in that there is a marked sexual dimorphism in the dorsal setae, not seen in other *Erythraeus*. Probably subsequently they will have to be separated generically, but the author is not prepared to do this until the larva is known for certain (see also remarks for *Erythraeus oudemansi*).

Collecting has been done by the author at Glen Osmond, from 1936 to 1940. The type is in the South Australian Museum. Other specimens recorded, in the author's collection.

ERYTHRAEUS OUEMANSI (Womersley 1936). Fig. 8, A-G.

*Bochartia oudemansi* Womersley 1936, *J. Linn. Soc. Lond.*, Zool., 40 (269): 121.

*Re-description of Larva (Type).* Fig. 8, A-G: Red. Body ovoid, length 1176 $\mu$ , width 910 $\mu$ . Dorsal scutum evenly rounded posteriorly, concave anteriorly, with rounded anterolateral angles, length 173 $\mu$ , width 167 $\mu$ . Scutum with 2 pairs of ciliated sensillary setae, anterior 45 $\mu$  long, posterior 89 $\mu$ ; with 2 pairs of non-sensillary setae, stout, ciliated, anterior pair placed very slightly anterior to the anterior sensillae, 64 $\mu$  long, posterior pair at the level of the middle of the shield, 70 $\mu$  long; Eyes 2+2, each lateral pair on a distinct shield, just posterior and lateral to the scutum. Dorsum with about 124 setae, stout, blunt, strongly ciliated, 40-95 $\mu$  long, the posterior setae being the longer; the ciliations are strong, acute. Setae arranged in obscure lines across the dorsum. Venter: just behind coxae I a pair of tapering pointed very slightly ciliated setae 75 $\mu$  long; between the levels of coxae II and III a similar pair 52 $\mu$  long; behind coxae III about 45 setae, the anterior of these being pointed, finely ciliated, 47-79 $\mu$  long, the posterior setae blunt, ciliated, 52-70 $\mu$  long. Each coxa with one seta: on I arising near its posterolateral angle, ciliated, pointed, 129 $\mu$  long; on II arising near middle of its posterior border, ciliated, blunt, 37 $\mu$  long; on III arising near middle of its anterior border, ciliated, blunt, 61 $\mu$  long. Legs long and thin: I 1340 $\mu$  long, II 1255 $\mu$ , III 1550 $\mu$  (all including coxae and claws). Each trochanter with 2 setae. Tarsus I 184 $\mu$  long by 25 $\mu$  high, strongly chitinized, and provided with a strong tapering pointed sensory rod, with very fine adpressed ciliations, and which arises from a pit at the distal end of the dorsum of the tarsus; all the other setae of the tarsus are ciliated; tarsal empodium is strong, ridged, falciform and over-reaches the two lateral claws; anterior claw bent over ventrally terminally; it has many branching ventral ciliations and a number of fine adpressed dorsal ciliations; posterior claw is brush-like with branching ventral ciliations. Metatarsus I 350 $\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 7 setae respectively. Palpal claw trifurcate. Palpal tarsus as figured.

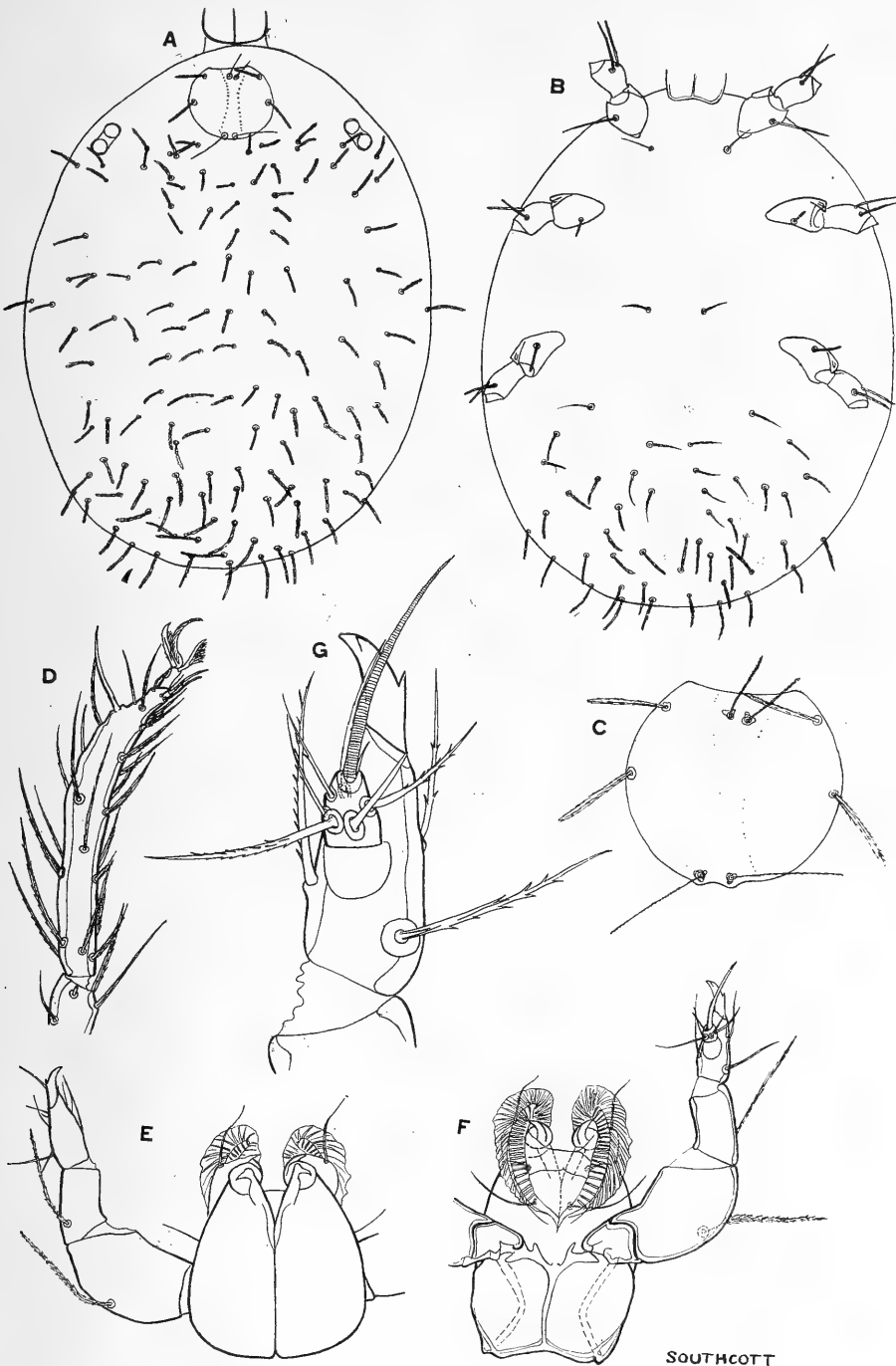
*Localities:* Type specimen from Adelaide, South Australia, 1934 (H. Womersley); Glen Osmond, South Australia, occurring throughout March-May, commonest in April, many specimens, in soil, on trunk or under bark of *Eucalyptus rostrata*, from 1935 to 1940 (R.V.S.); specimens also collected in Adelaide (R.V.S.).

*Biology.*

This is the largest larval erythraeid mite found at Glen Osmond. I have never taken it parasitic in the field, nor have I been able to feed it or get it to parasitize any host. The larvae are found in fair numbers. Fully-fed larvae are rarely taken in the field (I have seen only 2 such specimens; one is the type).

*Remarks:* A comparison of the times of occurrence of this larva with those of the nymphs and adults of *Erythraeus imperator* at the same tree at Glen Osmond suggests strongly that *E. oudemansi* (Wom. 1936) is the larva of *E. imperator* (Hirst 1928). *E. oudemansi* also is the largest larva occurring there, all others being much smaller. *E. imperator* is the largest adult occurring there, and its eggs are large, being the only ones for the species of *Erythraeus* at that situation comparable in size with the larval *E. oudemansi*. At the situation, in addition, the larvae of all the adults of *Erythraeus*

have been worked out, except 2 species—*E. imperator* and the much smaller *Erythraeus guttatus*, n. sp. (q.v.).



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Fig. 8.—*Erythraeus oudemansi* (Womersley 1936). A, Dorsum of fully-fed specimen (type); B, Venter of same; C, Dorsal scutum; D, Tarsus I; E, Capitulum from above; F, same from below; G, Tip of palp. (All figures from type.)

Despite the virtual certainty of *imperator* and *oudemansi* being identical, the author is not prepared to synonymize them until the relationship is proved experimentally.

*E. oudemansi* differs considerably from the other larvae of the genus found at Glen Osmond, in having only 2 pairs of non-sensillary setae to the scutum (like the genotype of *Bochartia* Oudemans 1910—*B. kuyperi* Ouds. 1910), 2 setae to the trochanters, and in that the palpal claw is trifurcate, not bifurcate, and probably subsequently it will have to be generically separated from *Erythraeus* s. str.



Fig. 9.—*Erythraeus reginae* (Hirst 1928). Larva. A, Dorsum; B, Venter; C, Tarsus I; D, Capitulum from above, less palpi; E, Capitulum from below (with dorsal view of palp on right); F, Palpal tarsus.

The most promising method of rearing this larva to the nymphal stage appears to be by capturing the rare fully-fed larvae in the field as was done with *Microsmaris* and other Erythraeidae. The type specimen is a large well-fed mite; unfed specimens measure 500–600 $\mu$  long by 370–430 $\mu$  wide. One from Glen Osmond 25th Mar., 1936, was 1300 $\mu$  long by 770 $\mu$  wide.

Type in the South Australian Museum; the other specimens in author's collection.

*ERYTHRAEUS REGINÆ* (Hirst 1928). Figs. 7, G–J; 9, A–F; 10, A, B; 11, A–G.

*Leptus reginæ* Hirst 1928, *Ann. Mag. nat. Hist.*, (10) 1(4): 569.

*Erythraeus reginæ* Womersley 1934, *Rec. S. Aust. Mus.*, 5(2): 219.

*Adult.* Fig. 7, G, H: This was originally described by Hirst from material from Adelaide, South Australia, without figures. It was re-described and figured by Womersley. The dorsal setae are re-figured here. Additional description from the syntype material: Dorsal setae have a broad pigmented convex dorsum, and on their under side a prominent keel, dorsal setae with many short broad dagger-shaped ciliations, and are 35–60 $\mu$  long. Some of the dorsal setae are unpigmented, but these areas are not conspicuous (unlike the prominent white spots of *E. guttatus*, n. sp.). The crista has a broad shield which carries the normal dorsal setae. Sensillary setae to crista robust, tapering, with very fine adpressed ciliations, anterior 155 $\mu$  long, posterior 170 $\mu$  long.

*Egg* (laid by adults from Glen Osmond, South Australia). Fig. 11, D–G: Red. Smooth when first laid. Spheroidal, 300 $\mu$  long by 240 $\mu$  wide. Chorion never pigments deeply. Several weeks after the eggs are laid the chorion becomes ridged, and later the deutovum stage appears.

*Description of Larva* (from egg laid by adult which was taken at Glen Osmond). Fig. 9, A–F: Red. Body ovoid, 230 $\mu$  long by 195 $\mu$  wide (unfed; a fully-fed animal measured 920 $\mu$  long by 625 $\mu$  wide). Dorsal scutum nearly circular, except for its concave anterior border, 102 $\mu$  long by 119 $\mu$  wide; with 2 pairs of very faintly ciliated sensillary setae, anterior 66 $\mu$  long, posterior 74 $\mu$ ; with 3 pairs of blunted ciliated non-

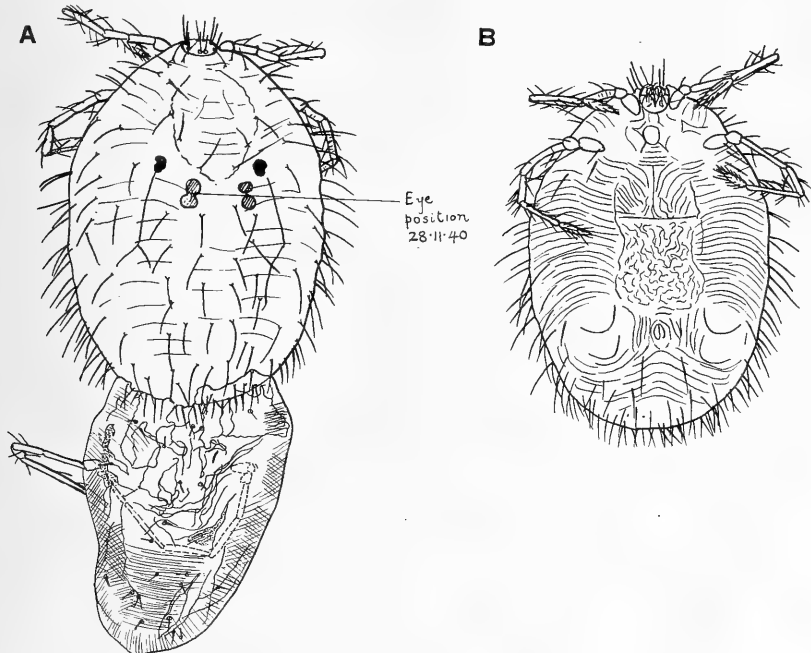


Fig. 10.—*Erythraeus reginæ* (Hirst 1928). Post-larval pupa (pupa I), with cast larval skin still attached. A, Dorsal view, transmitted light; B, Ventral view, reflected light. (The figures are taken from ACA 713AO on 24.xi.40; the position of the developing eyes on 28.xi.40 is marked in; they were in the same position on 1.xii.40.)

sensillary setae, arising as figured, anterior  $91\mu$  long, middle  $79\mu$ , posterior 2 stouter than the other 4,  $54\mu$  long. Eyes 2+2, anterior eye the larger. Dorsum with 32 stout blunted ciliated setae,  $35-45\mu$  long, arranged 6, 4, 6, 4, 2, 6, 4; distally on each seta the ciliations are broad and dagger-shaped, proximally they are sharper; the ciliations overlap like the bracts of a pine cone. Venter: between coxae I are 2 slender simple pointed setae  $54\mu$  long; between coxae II and III a pair of pointed ciliated setae  $39\mu$  long; behind coxae III a curved row of 4 ciliated setae,  $37\mu$  long, the medial 2 are pointed, the lateral 2 stronger, blunt; then 2 rows of 4 blunted ciliated setae,  $30-34\mu$  long. Each coxa with one seta: on I pointed, with adpressed ciliations,  $84\mu$  long; on II blunt, with adpressed ciliations,  $36\mu$  long; on III similar,  $36\mu$  long. Legs long and thin: I  $955\mu$  long, II  $845\mu$ , III  $1005\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $150\mu$  long by  $26\mu$  high. Ventral tarsal setae ciliated, dorsal setae simple. Tarsal empodium strong and falciform, with longitudinal ridges along its sides, and with a few faint ventral ciliations, and over-reaches the two lateral claws; anterior claw straight except for a weak terminal hook, with many branching ventral and some short dorsal ciliations; posterior claw retroflexed, with branching ventral ciliations. Metatarsus I  $262\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively. Palpal claw with a strong dorsal tooth. Palpal tarsus as figured.

*Description of Post-Larval Pupa (Pupa I)* (Specimen ACA 713AO). Fig. 10, A, B: Red. Length  $1025\mu$ , width  $705\mu$ . Ovoid, convex dorsally, flattened ventrally, with the normal protuberances which contain the developing tarsi of the nymph. Ventrally there is the normal central recessed area. Pupa patterned with fine ridges as figured. Setae tapering, pointed, with fine adpressed ciliations, to  $145\mu$  long.

*Description of Nymph* (from bred specimens ACA 713AO and ACA 713AP). Figs. 7, I, J; 11, A: Red. Body oval; size (freshly emerged)  $895\mu$  long, by  $640\mu$  wide. Crista, sensillary setae, eyes as in adult (although the nasus is blunter). Anterior sensillary setae  $108\mu$  long, posterior  $142\mu$ . Distance between centres of anterior and posterior sensillae  $375\mu$ . Dorsal setae as figured, elongate, very little expanded, pigmented, with serrations dorsally, keeled ventrally,  $32-45\mu$  long, bearing little resemblance to the adult dorsal setae. Palp similar to adult. Palpal claw ventrally with fine basal teeth. Legs: I  $2300\mu$  long, II  $1350\mu$ , III  $1680\mu$ , IV  $2750\mu$  (including coxae and claws). Tarsus I  $255\mu$  long by  $96\mu$  high; metatarsus I  $505\mu$  long.

When fully-fed ACA 713AO measured 2.06 mm. long by 1.28 mm. wide.

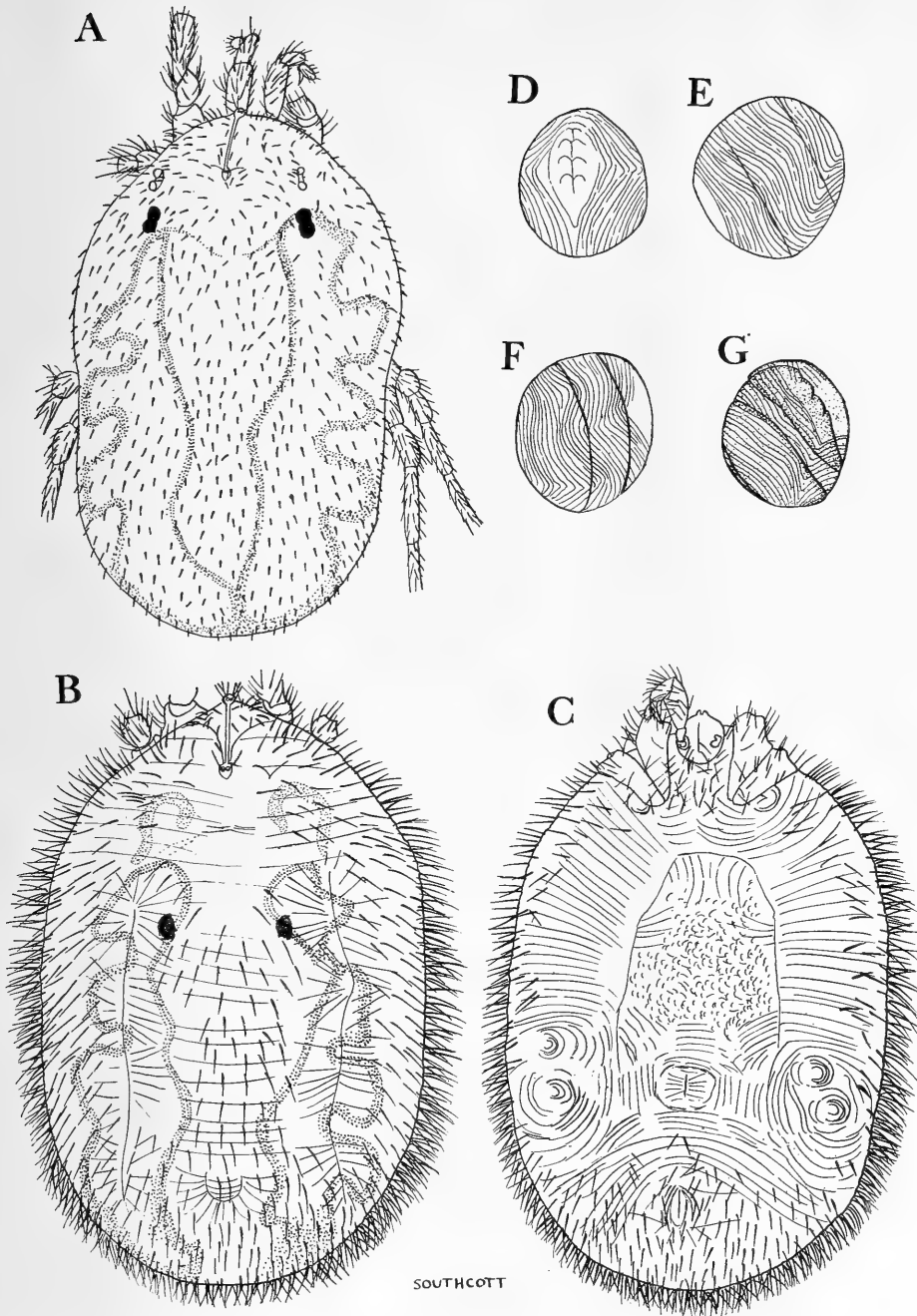
*Description of Pupa II* (ACA 713AO). Fig. 11, B, C: Red, aloid, similar to Pupa I, but larger and with more setae. Length  $2200\mu$ , width  $1450\mu$ . Setae stout, tapering, pointed, with fine adpressed ciliations, each seta arising from a papilla; setae  $60-145\mu$  long. (The adult that hatched out from this Pupa II was  $1900\mu$  long by  $1490\mu$  wide.

*Localities* (larvae only): South Australia: Cape du Couëdic, Kangaroo Island, one specimen, on a psocid, 4th Dec., 1934 (H. Womersley); Flinders Chase, Kangaroo Island, one specimen on a larval homopteron, Dec., 1934 (H.W.); Glen Osmond, 27th Nov., 1936 (1 specimen), 30th Oct., 1937 (1 specimen), on a larval jassid, 2nd Nov., 1941 (1 specimen, free) (all R.V.S.); see also the records of the specimens reared (below).

#### *Biology.*

At Glen Osmond, and elsewhere around Adelaide, adults are found from November to March (R.V.S., 1934-1940); the eggs are laid in December-March, and hatch in the following September-November, mostly November (eggs laid on two occasions by adults under observation, and also eggs taken in the field, have hatched to larvae). The eggs are laid in large batches, loosely aggregated. Experimentally the deutovum stage has been seen in early October, for eggs hatching from 10th to 18th Nov., 1938. (Experimentally the larvae will attach to the psocopteron *Troctes divinatorius*, but they are not found on this host in the field.)

Results of successful rearing experiments with batches of larvae hatching from eggs taken in the field at Glen Osmond some months before are set out in the following table. Batches of 5-8 larvae were generally used. Three experiments were successful



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Fig. 11.—*Erythraeus reginae* (Hirst 1928). A, Fully-fed nymph, dorsal view (ACA 713AO); B, C, Post-nymphal pupa (pupa II) (ACA 713AO), with some of the cast nymphal skin still attached; B, Dorsal; C, Ventral; D-G, Eggs, deutovum stage.

in rearing nymphs, and one of these was reared through to an adult. One of each of the batches recorded in the table was reared, although nearly all larvae attached, often more than once:

Batch Number.	ACA 713AO.	ACA 713AP.	ACA 713AR.
Started with .. .. .	5 larvae 30.x.40.	5 larvae 30.x.40.	8 larvae 5.xi.40.
Attached finally to jassid	6.xi.40.	5.xi.40.	Attached and reattached.
Finally detached .. .. .	One left alive on 16.xi.40, removed artificially after the jassid died.	One larva left alive on 10.xi.40, now detached, jassid still alive.	One larva alive on 14.xi.40.
Larva immobile .. .. .	18.xi.40 (2).†	13.xi.40 (3).	18.xi.40 (2).
Pupa I .. .. .	20.xi.40 (12). Length, 1,025 $\mu$ .* Width, 705 $\mu$ .	16.xi.40 (13).	20.xi.40 (12).
Nymph emerged .. .. .	2.xii.40 (21). Length, 810 $\mu$ . Width, 640 $\mu$ .	29.xi.40 (—). Killed at once.	2.xii.40 (—). Killed at once.
Nymph became immobile	21.xii.40. Length, 2,060 $\mu$ .* Width, 1,280 $\mu$ .	—	—
Pupa II .. .. .	23.xii.40 (15). Length, 2,200 $\mu$ .* Width, 1,450 $\mu$ .	—	—
Adult emerged .. .. .	7.i.41 ♀. Length, 1,900 $\mu$ . Width, 1,490 $\mu$ . (Died on 16.i.41.)	—	—

\* Stage figured in this paper.

† The figures in brackets indicate the total time in days spent in that stage.

The above experiments may be summarized as follows: When fully-fed, the larva remains in an immobile state for 2–3 days, then pupates; the pupa I stage lasts 12–13 days; the nymphal stage lasts 21 days. The adult lives for several weeks at least.

*Remarks:* The only stage of this species known previously was the adult, the larval and all the other stages of the life-history recorded above being previously completely unknown.

For remarks on the systematic position of *E. reginae*, see under *E. antepodianus* (Hirst 1928), to follow.

#### ERYTHRAEUS ANTEPODIANUS (Hirst 1928).

*Leptus antepodianus* Hirst 1928, *Ann. Mag. nat. Hist.* (10) 1(4): 570.

*Erythraeus reginae* Womersley 1934 (part), *Rec. S. Aust. Mus.*, 5(2): 219.

The type locality of this species was Tanunda, South Australia (recorded as "Tununda" by Hirst). It is very close to the preceding species, with which it was synonymized by Womersley. I have had the opportunity of examining the type of *E. antepodianus* and the co-types (♂ and ♀) of *E. reginae* in the South Australian Museum, and agree with Hirst's action in making of this a distinct species.

A larval species quite close to the larva of *Erythraeus reginae*, *Erythraeus stuarti*, n. sp., described later in this paper, has been found at Attack Creek, in the Northern Territory. At Tennant Creek, about 40 miles south, an adult almost indistinguishable from *E. reginae* has been found, and this is quite likely the adult of *Erythraeus stuarti*, n. sp. There are minute differences in the structure of the dorsal setae between this adult (which is not described in this paper) and *E. reginae*, and there are also comparable minute differences in *E. antepodianus*. Other somewhat similar adults from eastern Australia show other minute differences in the dorsal setae. It has not been possible to work out the taxonomy of this complex group in this paper, and in fact it may have

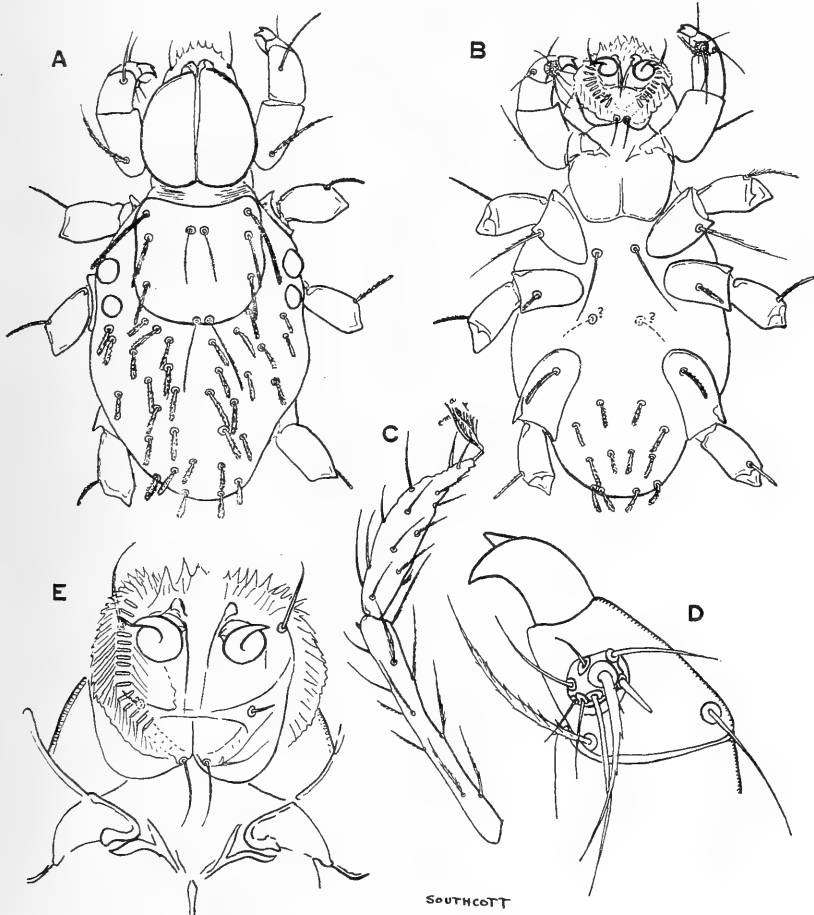


to wait until the larvae are known. The separation (later in this paper) of *Erythraeus guttatus*, n. sp., which is related to this complex but can be separated easily, is a further indication of the complexity of the group. The most promising differences upon which the further species of adults can be separated out appear to be the minute structure of the dorsal setae and the arrangement of the dorsal patches of unpigmented setae.

The separation of *E. antepodanus* from *E. reginae* was not attempted in the key. Hirst distinguished them thus: (*E. antepodanus*) . . . "body setae . . . not shaped like those of *L. reginae*, having the distal part narrower, more drawn out, and sharply pointed. Terminal claw of penultimate segment of palp poorly developed, being weaker than that of *L. reginae*. Palpal tarsus club-shaped and swollen, being much stouter than that of *L. reginae*".

ERYTHRAEUS STUARTI, n. sp. Fig. 12, A-E.

*Description of Larva (Type)*: Red. Ovoid. Body  $240\mu$  long by  $165\mu$  wide. Dorsal scutum squarish, concave anteriorly, sides straight, slightly concave between middle and posterior non-sensillary setae; scutum  $96\mu$  long by  $102\mu$  wide. Sensillary setae of scutum expand very slightly, are ciliated, anterior  $39\mu$  long, posterior  $54\mu$ . Non-sensillary setae of scutum are strongly ciliated, anterolateral  $56\mu$  long, middle  $43\mu$ , posterolateral (which resemble the normal dorsal setae)  $30\mu$ . Eyes 2+2. Dorsal setae 32, short, somewhat expanded, feather-shaped, with fine pointed ciliations, setae 24-34 $\mu$  long, arranged 4, 4, 4, 6, 4, 4, 5, 2. Venter: between coxae I a pair of long simple tapering pointed setae,



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Fig. 12.—*Erythraeus stuarti*, n. sp. Larva. A, dorsum; B, Venter; C, Tarsus I and metatarsus I; D, Tip of palp; E, Mouth-parts from below. (All figures from the type.)

$40\mu$  long; pair between coxae II and III are obscured in the type; behind coxae are 3 rows of setae, 4, 4, 4, similar to the dorsal setae. Seta on coxa I long, pointed, ciliated,  $68\mu$  long; on II short, blunt, ciliated,  $14\mu$ ; on III blunt, ciliated,  $24\mu$  long. Legs: I  $640\mu$  long, II  $545\mu$ , III  $710\mu$  (including coxae and claws). Tarsus I  $105\mu$  long by  $22\mu$  high; dorsal setae of tarsus simple, ventral setae ciliated. Tarsal empodium and claws weak

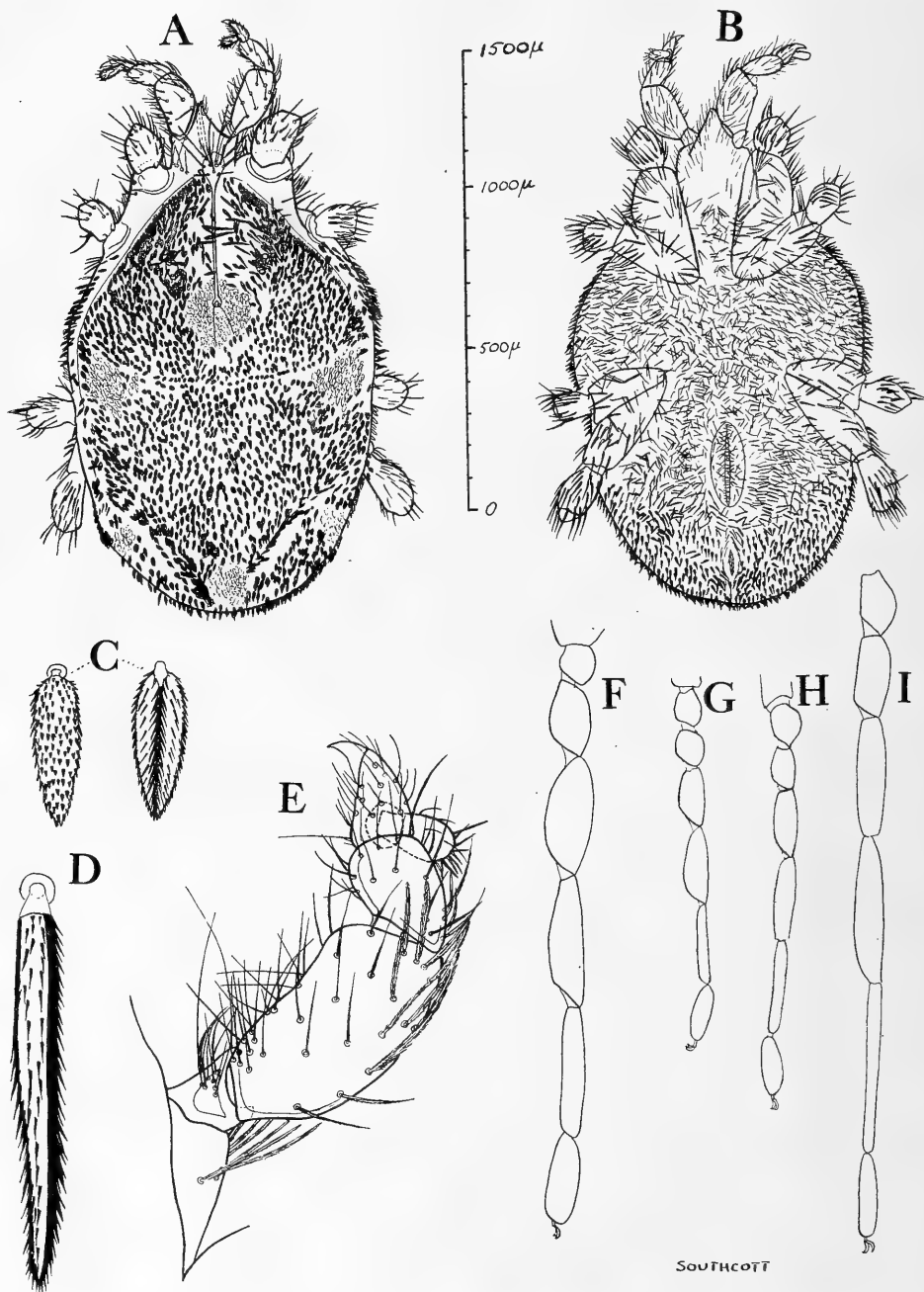


Fig. 13.—*Erythraeus guttatus*, n. sp. A, Dorsum; B, Venter; C, Dorsal seta  $34\mu$  long, from above and below; D, Longer dorsal seta,  $79\mu$ , from near crista; E, Palp; F, G, H, I, Outline of legs, I, II, III, IV (Figs. A, B, F-I all to scale given; all figures from the type.)

(see figure). Metatarsus I  $146\mu$  long. Capitulum as figured. Palpal claw bifurcate. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively.

*Locality:* Type larva from Attack Creek, Northern Territory, running free over the ground, 23rd June, 1942 (R.V.S.); in author's collection (ACA 1028).

*Remarks:* Close to *E. reginae* (Hirst 1928) larva. See remarks under *Erythraeus antepodianus*.

ERYTHRAEUS GUTTATUS, n. sp. Fig. 13, A-I.

*Description of Adult (Type):* Reddish, dorsally overlaid with black setae, and dorsally also with some prominent white spots. Body  $1330\mu$  long by  $870\mu$  wide. Crista normal; anterior sensillary area enlarged, bulbous, carrying 10 heavily ciliated long pigmented setae,  $50-146\mu$  long, as well as the 2 sensillary setae. Sensillary setae to crista pointed, with adpressed ciliations, anterior  $101\mu$  long, posterior  $104\mu$ . Crista surrounded by a broad shield. Eyes 2+2, on distinct shields, behind middle of crista. Most dorsal setae expanded, leaf-like, heavily pigmented, with many short serrations and a ventral ciliated keel, dorsal setae  $26-34\mu$  long by  $8-10\mu$  wide, some posterior setae longer, to  $57\mu$ ; over the anterior part of the dorsum the setae are stronger, mostly to  $47\mu$  long, but a few are much longer (Fig. 13, D), to  $80\mu$ . The conspicuous white spots on the dorsum are due to similar setae,  $40-73\mu$  long, but entirely unpigmented. The largest white patch surrounds the posterior sensillary area; there are 2 large white patches laterally, half-way along the body; another smaller one median in position, at the posterior end of the dorsum; 2 smaller still, posterolateral on dorsum, of only about 10 setae; a further middle median patch may be present midway between the antero-median and posteromedian patches (if present, it is of only 1-2 setae; absent from type). Dorsal setae encroach on the ventral surface of the body posteriorly, as far forward as the anus; otherwise venter with normal ciliated blunted setae. Legs long and thin: I  $2070\mu$  long, II  $1400\mu$ , III  $1490\mu$ , IV  $2380\mu$  (all including coxae and claws). Legs thickly covered with setae; on the distal half of tibia I and the distal  $\frac{1}{3}$  of tibia IV the setae are unpigmented, giving prominent white bands; otherwise setae black (except for the numerous fine sensory spines of the legs). Tarsus I  $280\mu$  long by  $100\mu$  high. Tarsal claws 2, strong, covered with fine ciliations. Metatarsus I  $360\mu$  long. Tarsus IV  $260\mu$  long by  $50\mu$  high. Metatarsus IV  $515\mu$  long. Palp as figured, claw ventrally with fine basal teeth.

*Locality:* Glen Osmond, South Australia. Adults are found from late November to mid-January, in leaf and bark debris at the bases of eucalypts (from 1936 to 1940; R.V.S.). Type taken on 1st Dec., 1937; in author's collection.

*Remarks:* This species comes within a complex which includes also *E. reginae*, *E. antepodianus* and *E. stuarti*, n. sp. (larval), etc. See remarks for *E. antepodianus*.

For the relationship of this species to *Erythraeus osmondensis*, n. sp. (larval), see remarks for that species.

One specimen laid eggs in mid-January, 1940, which did not hatch.

ERYTHRAEUS OSMONDENSIS, n. sp. Figs. 14, A-G; 15, A-D.

*Description of Larva* (from the two co-types). Fig. 14, A-G: Red. Body ovoid,  $270\mu$  long by  $180\mu$  wide. Dorsal scutum elongate-oval with the anterior margin concave; anterolateral angles rounded; scutum  $81\mu$  long,  $79\mu$  wide. Scutum with 2 pairs of ciliated sensillary setae, anterior  $24\mu$  long, posterior  $47\mu$ ; with 3 pairs of ciliated blunted non-sensillary setae, anterior  $62\mu$  long, middle  $46\mu$ , posterior  $46\mu$ . Eyes 2+2. Dorsum with about 32 setae, blunted, slightly tapering, strongly ciliated,  $37-44\mu$  long, arranged 4, 4, 4, 6, 5, 6, 3; the ciliations proximally placed on the setae are tapering and acute, distally they are blunted. Venter: between coxae I 2 pointed very slightly ciliated setae,  $28\mu$  long; between coxae II and III a similar pair  $32\mu$  long; behind coxae III are 3 rows of 4 setae, the first 4 tapering, ciliated, somewhat blunted, in a line convex posteriorly,  $28-30\mu$  long, the other 2 rows of stouter setae, similar to dorsal setae,  $29-30\mu$  long. Seta on coxa I long, tapering, pointed, ciliated,  $68\mu$  long; on II shorter, blunted, ciliated,  $44\mu$ ; on III similar,  $30\mu$ . Legs: I  $488\mu$  long, II  $464\mu$ ; III  $532\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $83\mu$  long by  $22\mu$  high, all of its setae

ciliated except a dorsal rod (the tarsus has also a small retroflected dorsolateral peg). Tarsal empodium falciform, over-reaching the claws, and with a few dorsal and ventral ciliations; anterior claw of tarsus slightly curved, with a weak terminal hook, and many branching ventral ciliations; posterior claw curved sinuously, with distal end retroflected, and with a few dorsal and many branching ventral ciliations. Metatarsus I  $106\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively. Palpal claw with a strong dorsal tooth. Palpal tarsus as figured.

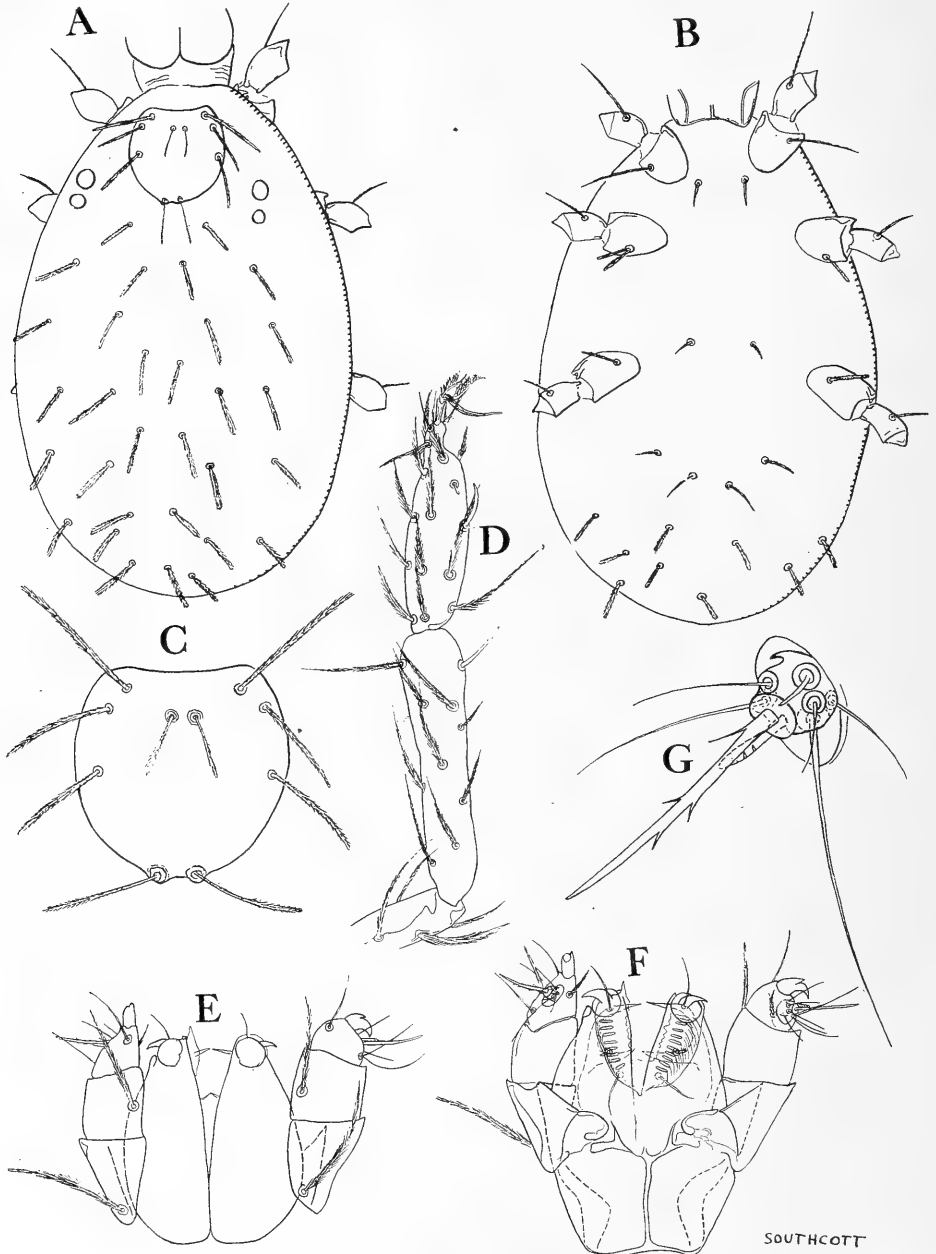


Fig. 14.—*Erythraeus osmondensis*, n. sp. Larva. A, Dorsum; B, Venter; C, Dorsal scutum; D, Tarsus I and metatarsus I; E, Capitulum from above (slightly distorted); F, Same from below; G, Palpal tarsus. (All figures from the co-types.)

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*Description of Post-Larval Pupa (Pupa I) (from ACA 1009).* Fig. 15, A, B: Red. Ovoid, flattened ventrally. Length  $650\mu$ , width  $445\mu$ . Dorsal setae lanceolate, with fine serrations, to  $90\mu$  long.

*Description of Nymph (from ACA 1009).* Fig. 15, C, D: Red, except for the white markings on the legs. Body length  $520\mu$ , width  $370\mu$  (unfed). Crista normal; sensillary setae slender, tapering, with fine adpressed ciliations, anterior  $91\mu$  long, posterior  $112\mu$ . Eyes  $2+2$ . Dorsal setae heavily pigmented, somewhat leaf-like, with rows of flattened ciliations, keeled ventrally,  $35-66\mu$  long. Some of the longer setae are present alongside the crista. None of the dorsal setae unpigmented. Palp normal, tibial claw ventrally with fine basal teeth. Legs: I  $1410\mu$  long, II  $925\mu$ , III  $1000\mu$ , IV  $1730\mu$  (all including coxae and claws). There are a few unpigmented setae distally on the dorsal side of tibia I; the setae on the distal  $\frac{1}{3}$  of tibia IV are unpigmented. Tarsus I  $169\mu$  long by  $63\mu$  high. Metatarsus I  $283\mu$  long. Tarsus IV  $167\mu$  by  $36\mu$ . Metatarsus IV  $400\mu$  long.

*Localities:* Mt. Osmond, South Australia, one larva, 1st Sept., 1933 (recorded by Womersley; slide labelled "1.10.33"), co-type; second co-type, one larva from Glen Osmond, 9th Nov., 1941, attached to a thrips (ACA 1010; R.V.S.); a further larva,

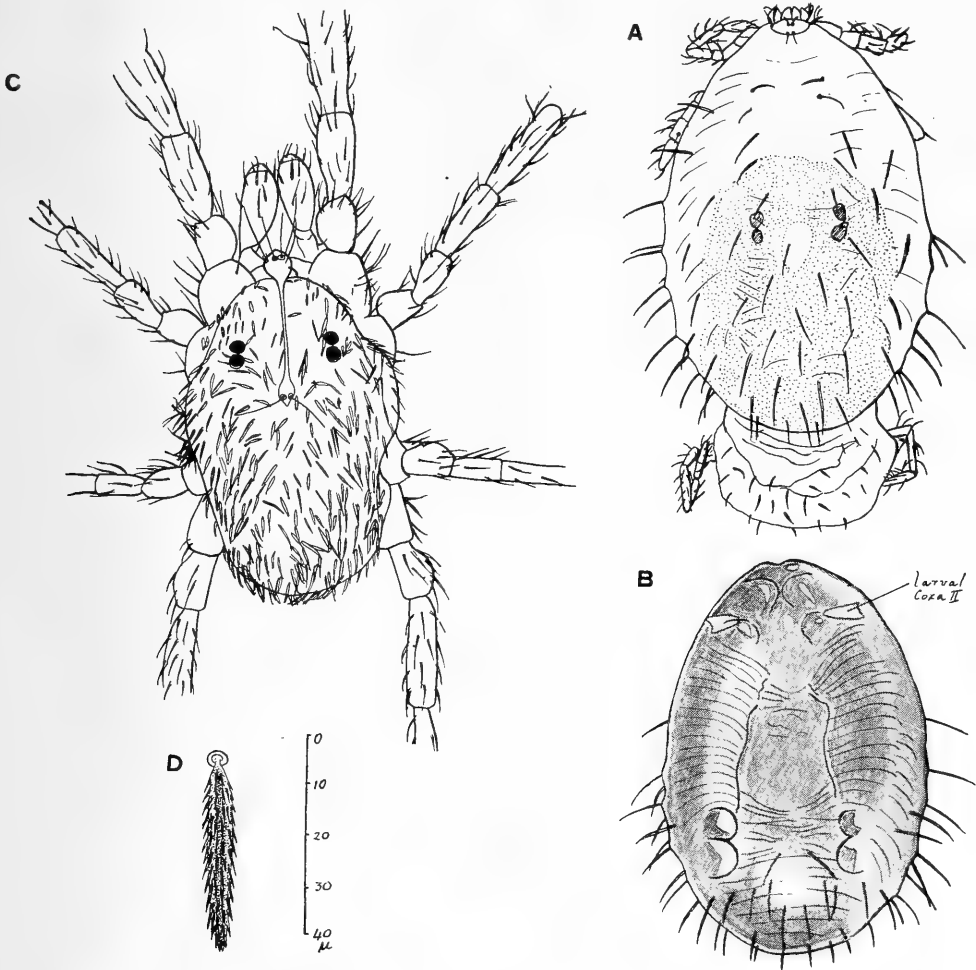


Fig. 15.—*Erythraeus osmondensis*, n. sp. A, B, Post-nymphal pupa (pupa II); A, Dorsal view, transmitted light, showing developing nymph, and with the cast larval skin still attached; B, Ventral view, reflected light; C, D, Nymph; C, Dorsal aspect; D, Dorsal seta, to scale shown. (All figures from ACA 1009; see text.)

attached to a thrips at Glen Osmond, 9th Nov., 1941, was reared to a nymph (specimen ACA 1009; see under biology).

*Biology.*

Specimen ACA 1009 when taken (9th Nov., 1941) had body  $290\mu$  long by  $165\mu$  wide (measured while still attached to the thrips). The thrips was kept alive on grass in a tube, and the mite remained attached until 16th Nov., 1941, when the thrips died. The mite left the host some hours later and wandered around the tube. Fresh jassids and thrips were given, but the mite did not attach to any. It became immobile on 17th Nov., 1941, and underwent ecdysis to pupa I on 19th Nov., 1941. The nymph emerged on 28th Nov., 1941, i.e., pupa I stage lasted 9 days. Food was provided for the nymph, but it died on 9th Dec., 1941, the body length then being  $575\mu$ , and width  $485\mu$ .

Specimen ACA 1010 was partly fed when captured, body length  $430\mu$ , width  $270\mu$ . It was dislodged on 9th Nov., 1941, and although fresh jassids and thrips were given, did not attach, and died on 24th or 25th Nov., 1941.

*Remarks:* The author considers it almost certain that *E. osmondensis*, n. sp. is the larva of *E. guttatus*, n. sp. There are strong resemblances between the nymph obtained and the adult *E. guttatus*; a method of elimination in considering the known adults and larvae at the base of this specimen of *Eucalyptus rostrata* lends very strong support to this belief. Until the relationship is proved, however, the larva is best considered separately.

Presumably thrips are the normal hosts of this larval species.

Minor teratological variations are encountered with this larva, particularly a doubling or forking of the seta on coxa I.

The first co-type was among the syntypes of *Bockartia longipes* Womersley 1934, but was not used in the original description and figures of that species (which is the larva of *Erythraeus urrbrae* Wom. 1934). The first co-type (damaged), from Mt. Osmond, in the South Australian Museum; the other specimens, including the second co-type, in author's collection.

ERYTHRAEUS PILOSUS (Hirst 1928). Figs. 16, A-F; 17, A-C.

*Leptus pilosus* Hirst 1928, *Ann. Mag. nat. Hist.*, (10) 1(4): 569.

*Erythraeus pilosus* Womersley 1934, *Rec. S. Aust. Mus.*, 5(2): 220.

*Description of Larva.* Fig. 16, A-F: Red. Body ovoid,  $250\mu$  long by  $190\mu$  wide (unfed). Dorsal scutum oval, flattened anteriorly,  $83\mu$  long by  $110\mu$  wide; with 2 pairs of simple slender sensillary setae, anterior  $94\mu$  long, posterior  $68\mu$ ; with 3 pairs of non-sensillary setae, anterior pair tapering, pointed, with adpressed ciliations,  $79\mu$  long, middle pair blunt, ciliated,  $60\mu$  long, posterior pair similar,  $48\mu$  long. Eyes 2+2, anterior the larger. Dorsum with about 29 setae, thin, tapering only slightly distally, blunted, and with slender pointed ciliations,  $31-45\mu$  long, arranged 4, 4, 4, 4, 6, 4, 3. Venter: between coxae I are 2 simple spiniform setae  $47\mu$  long; between coxae II and III are 2 similar setae,  $36\mu$  long; behind coxae III a transverse row of 4 spiniform slightly curved setae,  $28-38\mu$  long, then 4 blunted curved setae with fine adpressed ciliations,  $28-36\mu$  long, then 3 setae similar to the dorsal setae,  $20-28\mu$  long. Seta on coxa I long, spiniform,  $62\mu$ ; on II short, blunt, with adpressed ciliations,  $27\mu$  long; on III similar,  $29\mu$  long. Legs long, thin: I  $572\mu$  long. II  $517\mu$ , III  $662\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $94\mu$  long by  $21\mu$  high; none of tarsal setae ciliated; tarsal empodium strong, falciform, longitudinally ridged; anterior claw almost straight, with a weak terminal hook, and with many branching ventral ciliations reaching beyond the claw; posterior claw retroflexed, with branching ventral ciliations. Metatarsus I  $145\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively. Palpal claw with a strong dorsal tooth. Palpal tarsus as figured.

*Description of Post-Larval Pupa (Pupa I)* (from ACA 863). Fig. 17, A-C: Red. Shape ovoid, flattened ventrally. Body length  $720\mu$ , width  $485\mu$ . Setae lanceolate, with fine ciliations.

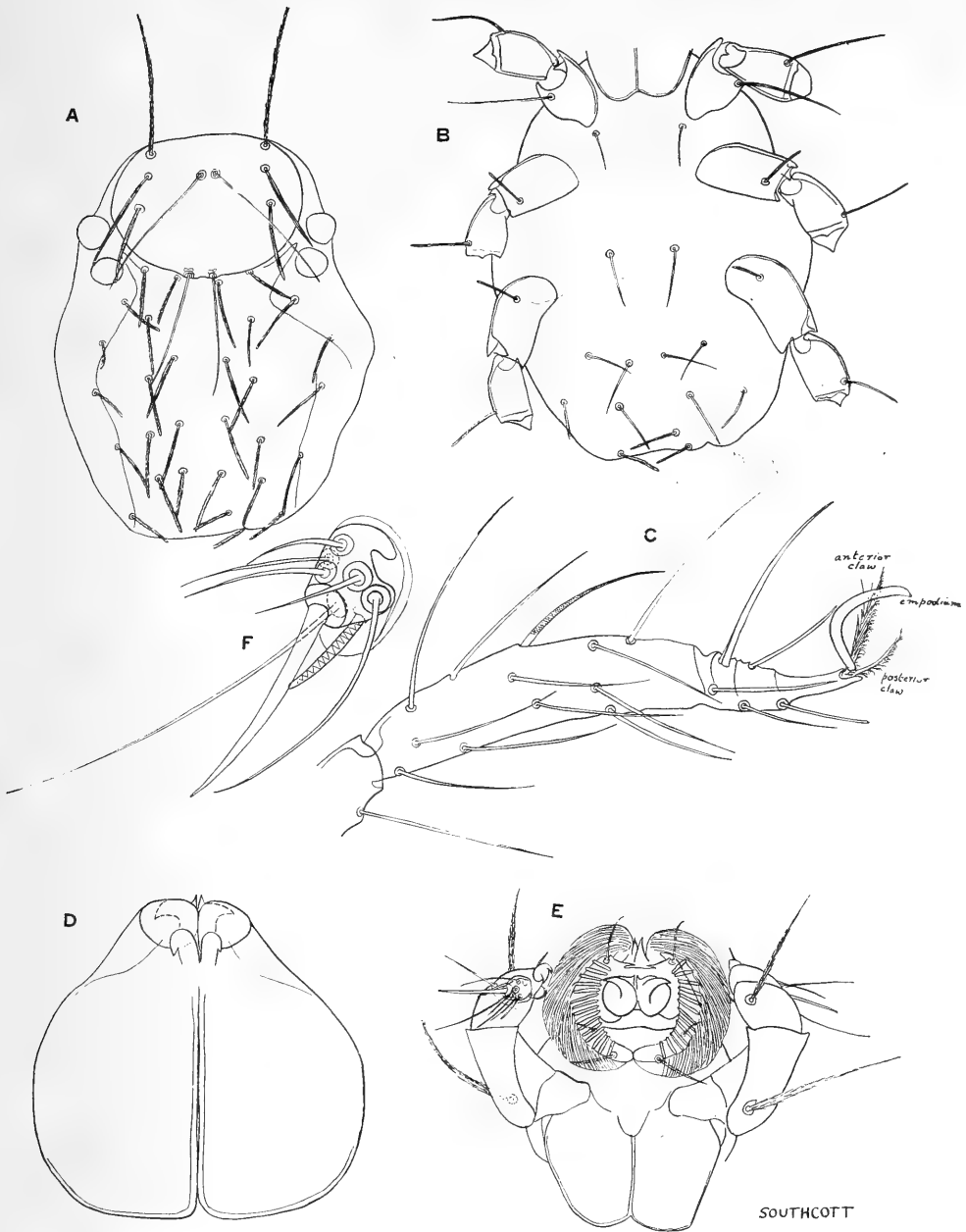


Fig. 16.—*Erythraeus pilosus* (Hirst 1928). Larva. A, Dorsum; B, Venter; C, Tarsus I; D, Capitulum, less palpi, from above; E, Capitulum from below (with dorsal view of palp on right); F, Palpal tarsus.

*Description of Nymph* (ACA 863, freshly emerged): Red. Body length  $510\mu$ , width  $280\mu$ . Distance between centres of anterior and posterior sensillae  $138\mu$ . Sensillary setae slender, anterior  $145\mu$  long, posterior  $170\mu$ . Dorsal setae long, fine, ciliated, pointed acutely (similar to adult),  $45\text{--}140\mu$  long. Legs long, with very long setae (legs of this specimen too crumpled for measuring). Tarsus I  $180\mu$  long by  $56\mu$  high; metatarsus I  $330\mu$  long.

*Localities* (larvae only): Glen Osmond, South Australia, 11th Mar., 1936, one specimen, free (R.V.S.), and several more at Glen Osmond in Nov., 1940, and Oct., 1941, attached to Psocoptera (*Myopsocus* sp.) and small Heteroptera, among débris at eucalypt bases (including ACA 863, below). For bred larvae see under biology.

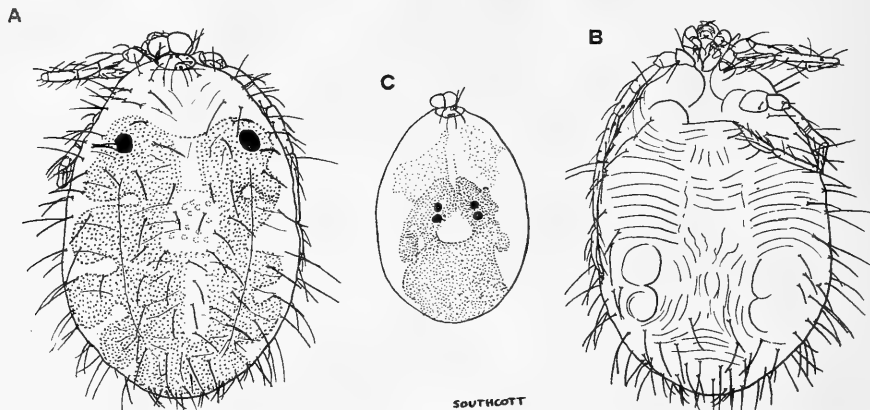


Fig. 17.—*Erythraeus pilosus* (Hirst 1928). Post-larval pupa (pupa I). A, above, containing developing nymph, and with the cast larval skin still attached (ACA 863 on 27.xi.40); B, Below, by reflected light; C, Dorsal view on 1.xii.40 to show further development of nymph. (All figures from ACA 863; see text.)

#### *Biology.*

The adults are found at Glen Osmond, South Australia, from January to August, but mainly in the autumn. The larvae occur from November to March, and the nymphs from April to May (in the field, but see ACA 863 below).

Three adults were taken at Glen Osmond on 8th May, 1938. Eggs were laid by next day; they were kept in a saturated atmosphere. By 21st Nov., 1938, one larva had hatched, and another by 27th Nov., 1938. Further larvae continued to hatch during December. (The eggs are similar to those of *E. reginae*, but the chorion is much more deeply pigmented.)

Larval specimen ACA 863 was taken at Glen Osmond on 16th Nov., 1940, attached to *Myopsocus* sp. It was still attached on 19th Nov., 1940. On 20th Nov., 1940, the host died and the mite left it, apparently less than full-grown. It was immobile on 21st Nov., 1940, and pupated on 24th to 25th Nov., 1940. The nymph emerged on 5th Dec., 1940. Thus the pupa I stage lasted 11–12 days.

*Remarks:* The type adult was from Dubbo, New South Wales, 7th Aug., 1927; in the South Australian Museum. The only stage of this species that was known previously was the adult; the larva and the other stages described above being completely new.

ERYTHRAEUS URRBRAE Womersley 1934. Figs. 18, A–G; 19, A–H.

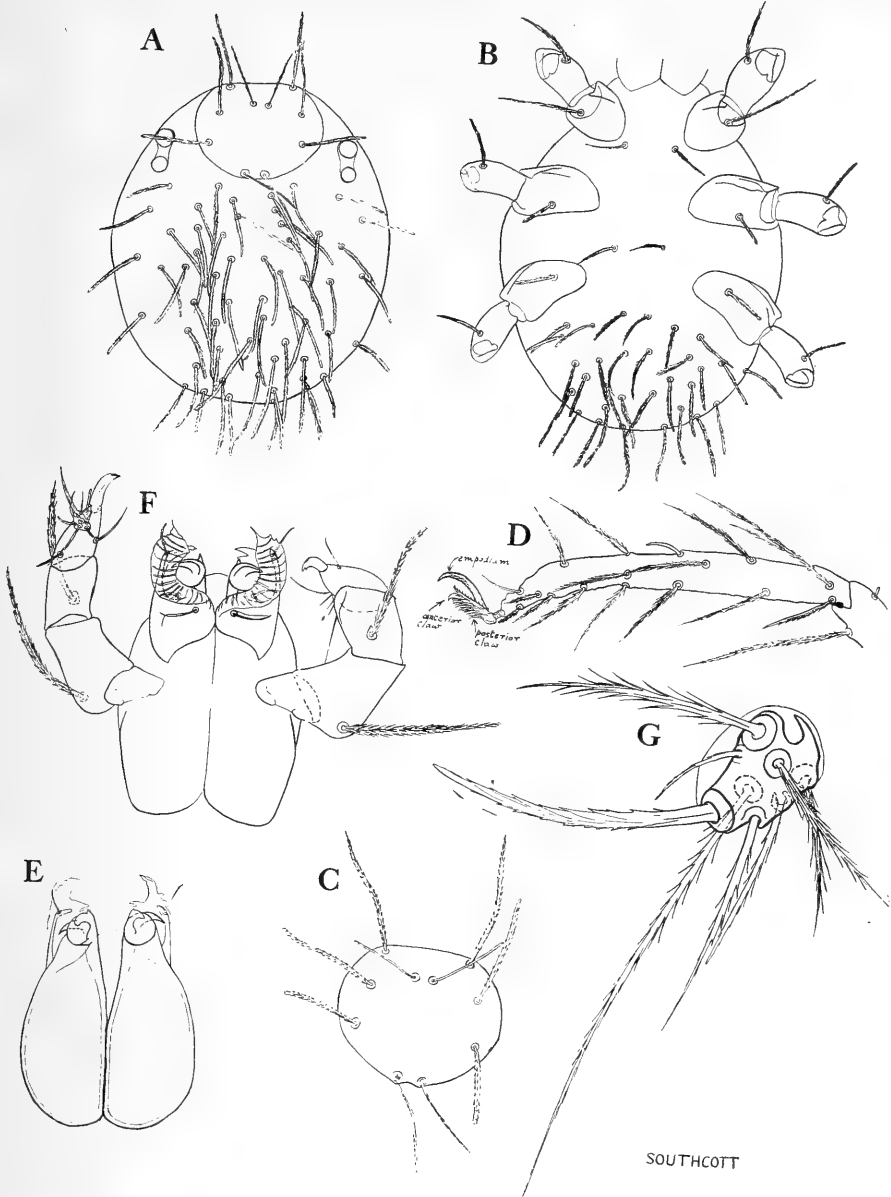
*Erythraeus urrbrae* Womersley 1934, *Rec. S. Aust. Mus.*, 5(2): 221.

*Bockartia ? longipes* Womersley 1934 (larval), *Ibid.*, 5(2): 252.

*Bochartia longipes* Womersley 1936, *J. Linn. Soc. Lond., Zool.*, 40(269): 120.

*Description of Larva* (from the 3 syntypes of *Bockartia ? longipes* Wom.). Fig. 18, A–G: Red. Body ovoid, length  $360\mu$ , width  $290\mu$ . Dorsal scutum oval, flattened anteriorly,  $108\mu$  long by  $136\mu$  wide; with 2 pairs of finely ciliated sensillary setae, anterior  $60\mu$  long, posterior  $73\mu$ ; with 3 pairs of strongly ciliated non-sensillary setae, anterior pair tapering, pointed,  $91\mu$  long, middle 2 somewhat blunted,  $83\mu$  long, posterior 2 are the stoutest, blunted,  $65\mu$  long. Eyes 2+2 on distinct shields; anterior eye the larger. Dorsum with 54 blunted ciliated long strong setae,  $52$ – $81\mu$  long; the ciliations taper and are almost acute. The setae are arranged in obscure lines across the dorsum. Venter: between coxae I a pair of tapering pointed ciliated setae  $44\mu$  long; between coxae II and III a





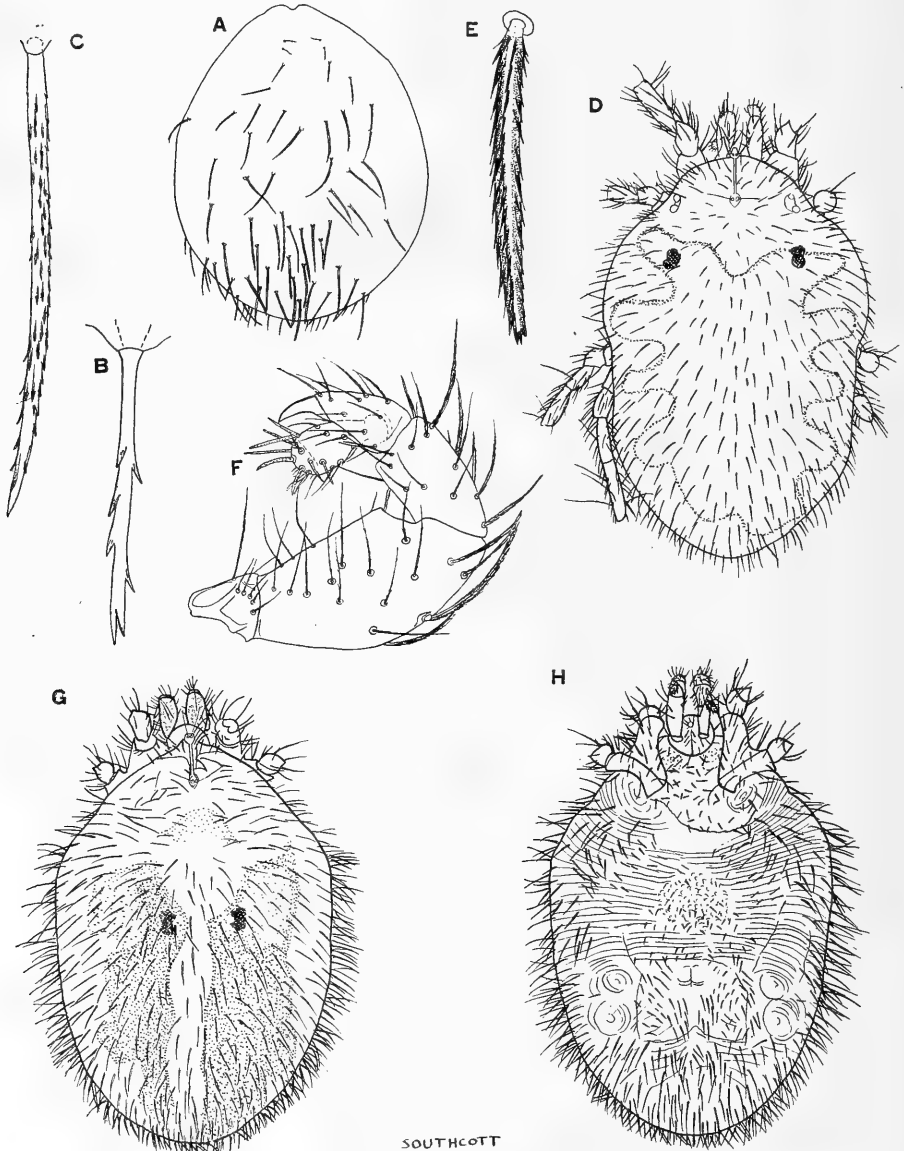
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Fig. 18.—*Erythraeus urbrae* Wom. 1934. Larva. A, Dorsum; B, Venter; C, Dorsal scutum; D, Tarsus I; E, Capitulum, less palpi, from above; F, Capitulum from below (with dorsal view of palp on right); G, Palpal tarsus. (All figures from the syntypes of *Bockartia ? longipes* Wom. 1934.)

stronger pair, heavily ciliated, tapering, pointed,  $50\mu$  long; just behind coxae III a row of 9 ciliated tapering setae, the central 2 pointed, other 7 less so,  $41-49\mu$  long; then 3 or 4 obscure rows of setae, 17 in all, tapering, somewhat pointed, ciliated,  $54-64\mu$  long. Each coxa with one seta: on I pointed, with adpressed ciliations,  $104\mu$  long; on II blunted, with adpressed ciliations,  $25\mu$  long; on III blunted and ciliated,  $39\mu$  long. Legs long and thin, I  $1072\mu$  long, II  $974\mu$ , III  $1120\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $171\mu$  long by  $23\mu$  high; empodium strong and falciform, with dorsal and ventral ciliations, and over-reaching the 2 lateral claws; anterior claw with a slightly curved shaft and terminal ventral hook, and with many

dorsal and ventral ciliations; posterior claw retroflexed, with branching ventral ciliations. All setae of the tarsus are ciliated, except one, which is strong, curved, simple, arising at about the middle of the dorsum of the tarsus. Metatarsus I  $293\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively. Palpal claw with a long strong dorsal tooth. Palpal tarsus as figured.

*Description of Post-Larval Pupa (Pupa I).* Fig. 19, A-C: Red. Ovoid, evenly rounded posteriorly, rather pointed anteriorly, and there notched. Length  $750-850\mu$ , width  $570-600\mu$  (several specimens). Dorsum convex, and with setae: 2 rows of 2 setae, slightly tapering, with stout ciliations,  $20-23\mu$  long; then 2 rows of tapering pointed



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Fig. 19.—*Erythraeus wirbrae* Wom. 1934.—A-C, Pupa I. A, Dorsal view of specimen  $750\mu$  long by  $600\mu$  wide; B, Dorsal seta  $23\mu$  long; C, Dorsal seta  $112\mu$  long. D-F, Nymph dorsal view, with outline of contained pigment mass (ACA 874 on 28:xii.40); E, Dorsal seta  $66\mu$  long; F, palp. G, H, Pupa II; G, Dorsal view, transmitted light (ACA 874 on 4.i.41); H, Venter of same, reflected light.

setae with adpressed ciliations,  $54\mu$ ,  $85\mu$  long respectively; then a number of rows of similar setae  $80$ – $112\mu$  long (lengths increasing posteriorly over the dorsum); the setae are free from ciliations in their proximal part. Ventral surface almost devoid of setae, except posteriorly, and there the setae are similar to those of the dorsal surface. Each seta of the pupa arises from a definite papilla.

*Description of Nymph* (freshly-emerged, i.e., unfed; description from ACA 19). Fig. 19, D–F: Body red, ovoid,  $600\mu$  long by  $380\mu$  wide. Anterior end of crista enlarged to a spheroidal bulb, wider than long, which carries the 2 sensillary setae, and continues downward and forward as a blunted conical nasus. Length of crista to front of bulb  $344\mu$ ; distance between centres of anterior and posterior sensillae  $308\mu$ . Bulb also carries 6 long ciliated tapering setae,  $100$ – $215\mu$  long. Sensillary setae long, thin, tapering, pointed, finely ciliated; anterior  $150\mu$  long, posterior  $190\mu$ . Eyes 2 + 2, each lateral pair on a distinct shield. Anterior eye level with middle of crista; posterior eye the more lateral. Dorsum thickly covered with dark tapering somewhat blunted ciliated setae,  $49$ – $146\mu$  long. Ventral setae more variable,  $36$ – $145\mu$  long, generally blunted (some anteriorly are pointed), less pigmented than the dorsal setae except at the posterior pole. External genitalia immature. Anus normal, bounded by 2 lateral crescentic laminae,  $56\mu$  long, each carrying 4 normal ventral setae  $30$ – $35\mu$  long. Legs long and thin: I  $2070\mu$  long, II  $1240\mu$ , III  $1420\mu$ , IV  $2200\mu$  (all excluding coxae). Tarsus I  $249\mu$  long by  $96\mu$  high, II  $152\mu \times 60\mu$ , III  $159\mu \times 54\mu$ , IV  $194\mu \times 49\mu$ . Tarsal claws 2, strong, falciform, covered with fine ciliations. Metatarsus I  $478\mu$  long, II  $308\mu$ , III  $390\mu$ , IV  $710\mu$ .

*Description of Post-Nymphal Pupa* (*Pupa II*) (ACA 864). Fig. 19, G, H: Red. Shape normal for pupae. Length  $1690\mu$ , width  $1120\mu$ . Dorsal setae lanceolate, pointed, finely ciliated, to  $155\mu$  long.

*Adult*: Described by Womersley in 1934. The dorsal setae are variable in length,  $63$ – $250\mu$  long.

*Localities* (larvae only): South Australia: Mt. Osmond, 1st Sept., 1933, the 3 syntypes of *Bockartia ? longipes*, collected by Womersley (slide labelled "1.10.33"); National Park, Belair, 7 specimens, 5th Nov., 1933 (H.W.): Cape du Couedic, Flinders Chase, Kangaroo Island, on a psocid, 1 specimen, 4th Dec., 1934 (H.W.); Glen Osmond, from August to January, but commonest from October to December, in vegetation (mostly *Avena fatua* L.) and on trunks and among foliage of *Eucalyptus rostrata*, etc., mostly running free, but also a considerable number has been taken attached to jassids, Psocoptera (*Myopsocus* sp.), etc., from 1936 to 1940 (R.V.S.); Adelaide, Nov., 1939 (R.V.S.). Victoria: Otway Forest, one specimen, parasitic upon an anystid mite, on the foliage of a tree-fern, 16th Jan., 1937 (R.V.S.).

### Biology.

At Glen Osmond the larvae occur as above; the adults occur from January to July, but are commonest from April to June; a very few adults have been taken in August and October.

Eggs taken under eucalypt bark at Glen Osmond on 23rd Feb., 1937, hatched out to a mixture of the larvae of *Erythraeus reginae* and *E. urrbrae* from 23rd Oct. to 6th Nov., 1937; other eggs from under eucalypt bark taken in Aug., 1937, hatched out to *E. urrbrae* larvae during Oct. and Nov., 1937.

Rearing experiments have been carried out with larvae taken parasitic on jassids and Psocoptera in the field. From these experiments a number of nymphs and two adults (one ♂ and one ♀) have been obtained (these adults, and the single adult of *E. reginae* obtained from a larva, are the first ever reared through from larvae in the family Erythraeidae, and have enabled the life-history of an erythraeid mite to be set out).

The life-history of *Erythraeus urrbrae* may be summarized as follows: the eggs are probably laid mainly in January and February, and hatch out to larvae over the following August to January; when fully-fed the larva leaves its host, and after remaining in an immobile state for 1–4 days, pupates; pupa I lasts 12–16 days, nymph 25–39 days, and pupa II 15–16 days. The adult lives for several weeks at least. The larva of *E. urrbrae* was previously known as *Bochartia longipes* Wom. 1934 (see introduction).

Details of the successful rearings are set out in Table 1 (all specimens were taken parasitic, on the hosts listed, at Glen Osmond, South Australia).

## ERYTHRAEUS WOMERSLEYI, n. sp. Fig. 20, A-H.

*Description of Larva (Type):* Red. Body ovoid,  $350\mu$  long by  $305\mu$  wide. Dorsal scutum flattened anteriorly,  $85\mu$  long by  $100\mu$  wide; with 2 pairs of slender almost simple sensillary setae with faint addressed ciliations, anterior  $47\mu$  long, posterior  $61\mu$ ;

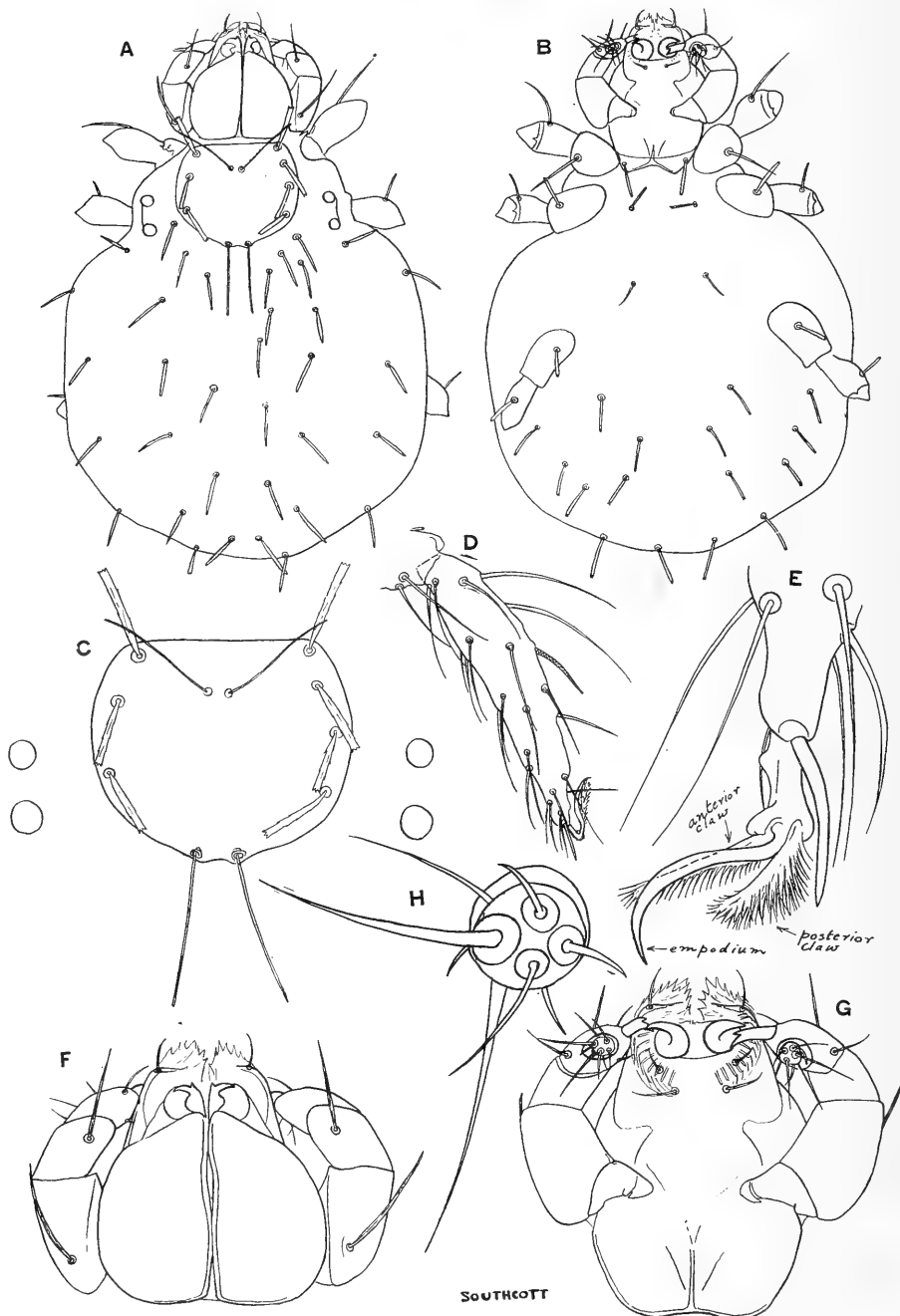


Fig. 20.—*Erythraeus womersleyi*, n. sp. Larva. A, Dorsum; B, Venter; C, Dorsal scutum and eyes; D, Tarsus I; E, Tip of tarsus I; F, Capitulum from above; G, Same from below; H, Palpal tarsus. (All figures from type.)

TABLE 1.

*Experimental Rearings of Stages of Erythraeus urbrae Wom., 1934, starting with Larvae.*

Experiment No.	Date Taken.	Left Host.	Became Dormant.	Pupa I.	Nymph Emerged.	Nymph Immobile.	Pupa II.
From foliage of <i>Eucalyptus rostrata</i> : each larva parasitic on a jassid.							
ACA 1 ..	7.xi.36	7.xi.36	— (?)	— (less than 27)	Before 4.xii.36 L, 605 $\mu$ ISD, 273 $\mu$	—	—
ACA 6A ..	7.xi.36	12.xi.36	— (?)	Probably 15.xi.36 (ca. 27)	12.xii.36 L, 510 $\mu$ ISD, 187 $\mu$	—	—
ACA 19 ..	12.xii.36	13.xii.36	15.xii.36 (2)†	17.xii.36 (13)	30.xii.36 L, 600 $\mu$ * ISD, 308 $\mu$	—	—
From under bark of <i>Eucalyptus cladoclyx</i> ; each larva parasitic on <i>Myopsocus</i> sp.							
ACA 864 ..	16.xi.40	17.xi.40	18.xi.40 (2)	20.xi.40 L, 830 $\mu$ W, 650 $\mu$ (15)	5.xii.40 (39)	13.i.41 L, 1,675 $\mu$ W, 1,080 $\mu$	14.i.41 L, 1,690 $\mu$ * W, 1,120 $\mu$ (16)
ACA 865 ..	16.xi.40	Remained at- tached even after pupation.	Indefinite. (?)	20.xi.40 L, 760 $\mu$ W, 595 $\mu$ (14)	4.xii.40 (11+)	Nymph died 15.xii.40	—
ACA 866	16.xi.40	20.xi.40	21.xi.40 (4)	25.xi.40 L, 805 $\mu$ W, 640 $\mu$ (12)	7.xii.40 L, 705 $\mu$ W, 500 $\mu$ ISD, 334 $\mu$ (21+)	Nymph died 28.xii.40	—
ACA 867 ..	16.xi.40	17-18.xi.40	18.xi.40 (2)	20.xi.40 (—)	Pupa killed with formalin.	—	—
ACA 868 ..	16.xi.40	16-17.xi.40	16-17.xi.40 (1-2)	17-18.xi.40 L, 860 $\mu$ W, 730 $\mu$ (15-16)	3.xii.40 (13+)	Nymph died 16.xii.40	—
ACA 869 ..	16.xi.40	16-17.xi.40	16-17.xi.40 (1-2)	17-18.xi.40 L, 845 $\mu$ W, 665 $\mu$ (14-15)	2.xii.40 (—)	Killed with alcohol 2.xii.40	—
ACA 871 ..	16.xi.40	16-17.xi.40	16-17.xi.40 (1-2)	17-18.xi.40 L, 915 $\mu$ W, 715 $\mu$ (15-16)	3.xii.40 (—)	Killed with alcohol 3.xii.40	—
ACA 874 ..	16.xi.40	16-17.xi.40	17-18.xi.40 (1-2)	19.xi.40 L, 795 $\mu$ W, 695 $\mu$ (16)	5.xii.40 (25)	28.xii.40 L, 1,590 $\mu$ * W, 1,025 $\mu$	30.xii.40 L, 1,590 $\mu$ * W, 1,090 $\mu$ (15)
ACA 877 ..	16.xi.40	16-18.xi.40	20.xi.40 (1)	21.xi.40 L, 840 $\mu$ W, 680 $\mu$ (—)	Pupa died.	—	—

\* Drawn or described (or both) in the text.

† Figures in brackets indicate the total time in days spent in that stage. *Note.*—The figures in the column for the nymphs are for the whole nymphal period.

L, body length; W, body width; ISD, inter-sensillary distance (distance between centres of anterior and posterior sensillae).



with 3 pairs of non-sensillary setae (in the type specimen an extra seta occurs on the right side), stout, with very faint addressed ciliations, and broadening at the end, which is toothed, anterior  $34\mu$  long, middle  $25\mu$ , posterior  $25\mu$ . Eyes 2+2. Dorsum with about 35 setae, stout, with addressed ciliations; most taper distally, the tip having small teeth, a few posterior setae expanding slightly distally to a more strongly toothed tip; setae  $26\text{--}36\mu$  long, arranged approximately 2, 4, 3, 5, 5, 2, 4, 4, 2, 4. Venter: between coxae I 2 stout truncated setae with very faint addressed ciliations and toothed at tip,  $26\mu$  long; between coxae II a similar pair  $20\mu$  long; between the levels of coxae II and III are 2 stout spiniform setae,  $16\mu$  long; behind coxae III are 4 rows each of 4 setae, parallel-sided and with truncated notched tips, stout or fairly stout, with very faint addressed ciliations, setae  $22\text{--}34\mu$  long. Each coxa with one seta: on I strong, curved, spiniform,  $42\mu$  long; on II stout, blunt, slightly tapering,  $23\mu$  long; on III similar,  $24\mu$  long. Legs long and thin: I  $525\mu$  long, II  $500\mu$ , III  $625\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $97\mu$  long by  $20\mu$  high; none of its setae ciliated; empodium somewhat slender, falciform, over-reaching the claws, not ciliated; anterior claw straight or slightly retroflexed, with many strong ventral ciliations; posterior claw retroflexed, strongly ciliated ventrally. Metatarsus I  $131\mu$  long. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 8 setae respectively. Palpal claw with a strong dorsal tooth. Palpal tarsus as figured.

*Locality*: Glen Osmond, South Australia, one specimen (type), 26th Oct., 1938, parasitizing an adult *Erythroides serratus*, in débris at base of *Eucalyptus obliqua* (R.V.S.); type in author's collection.

Genus LEPTUS Latreille 1796.

*Préc. Car. Ins.*, 1796, 177.

*Genotype*: *Acarus phalangii* de Geer 1778.

LEPTUS ANOMALUS, n. sp. Fig. 21, A-H.

*Description of Larva (Type)*. Fig. 21, A-H (21, F from another specimen): Red. Small. Body ovoid,  $175\mu$  long by  $145\mu$  wide. Dorsal scutum triangular, with rounded angles, anterior margin slightly concave, posterolateral margins slightly convex; scutum  $56\mu$  long by  $83\mu$  wide. Anterior part of shield thin, striated transversely, and carries the slender finely ciliated anterior sensillary setae  $33\mu$  long; posterior sensillary setae similar,  $66\mu$  long; 2 pairs of non-sensillary setae, as figured, to the shield, anterior pair slightly clavate, truncated, with many strong ciliations, posterior pair similar but parallel-sided,  $33\mu$  long. Eyes 1+1, near posterolateral borders of shield. Dorsum with about 88 stout slightly clavate truncated setae with many strong ciliations,  $22\text{--}35\mu$  long; the most anterior setae are one on each side, between the eye and the shield. Venter: between coxae I are 2 bushy setae, with many long ciliations,  $27\mu$  long; between coxae II 2 pairs of similar but more bushy setae, anterior pair  $20\mu$  long, posterior  $16\mu$ ; just behind coxae II 2 bushy setae,  $18\mu$  long; between coxae III 2 similar setae,  $20\mu$ ; then a curved row of 4, the medial 2 bushy,  $22\mu$  long, lateral 2 narrower,  $28\mu$  long; then a row of 6 setae, the lateral 2 similar to the lateral 2 of the previous row,  $26\mu$  long, medial 4 bushy, elongate-oval,  $23\mu$ ; then 13 setae in 2 rows: 6, 7, elongate, expanding slightly distally, strongly ciliated,  $26\text{--}27\mu$  long. Each coxa with one seta: on I long, strongly ciliated, slightly tapering,  $45\mu$  long; on II short,  $18\mu$ , blunt, bushy, with fairly long ciliations; on III blunt, strongly ciliated,  $22\mu$  long. Legs long and thin: I  $530\mu$  long, II  $430\mu$ , III  $530\mu$  (including coxae and claws). Each trochanter with one seta. Tarsus I  $95\mu$  long by  $26\mu$  high; empodium fairly strong, falciform, simple, over-reaching the claws; anterior claw strong, falciform, with a few faint ridges along its sides; posterior claw strong, sinuously curved, with a number of long strong ventral ciliations and 2 strong dorsal ciliations; all tarsal setae ciliated, except for a curved tapering rod that arises two-thirds along the dorsum of the tarsus. Metatarsus I  $125\mu$  long. Capitulum as figured, dorsally flask-shaped with a concave posterior margin. Palpal femur, genu, tibia, tarsus with 1, 2, 3, 8 setae respectively. Palpal claw strong and simple (no accessory teeth). Palpal tarsus as figured.

*Locality*: Glen Osmond, South Australia, 28 specimens, between Sept. and Nov., 1937 (R.V.S.)—see under *Erythroides clavatus*, n. sp. (larval), biology (1) (p. 16), for the

origin of these. One specimen taken as type; from this the descriptions and figures have been taken, except Fig. 21, F. The mandibles of the type specimen are distorted by compression. All specimens in author's collection.

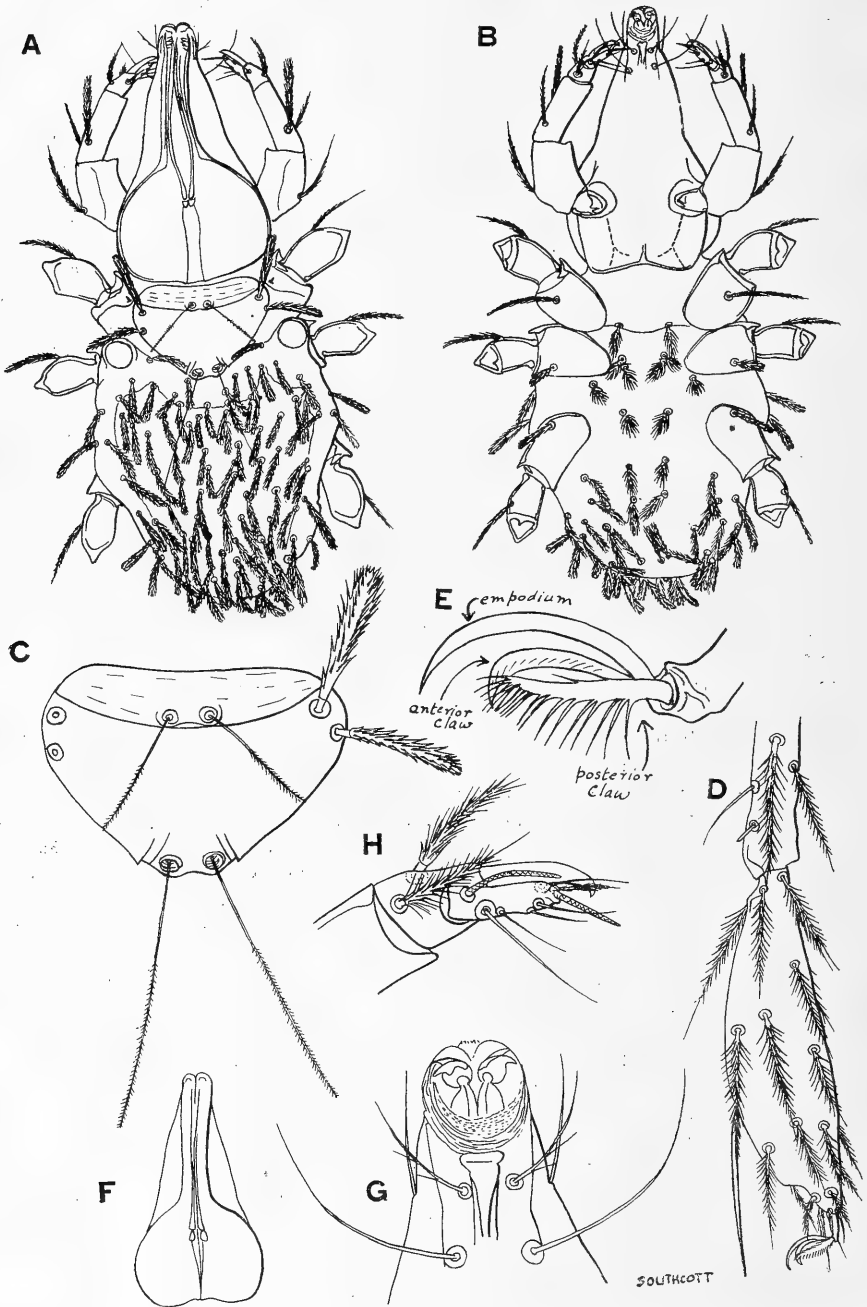


Fig. 21.—*Leptus anomalus*, n. sp. Larva. A, Dorsum (capitulum distorted); B, Venter; C, Dorsal scutum; D, Tarsus I; E, Tip of tarsus I; F, Capitulum from above, undamaged specimen; G, Mouth-parts from below. (All figures except F, from type.)



*Remarks:* The approximation of the coxae shown in the figures is of no taxonomic significance, indicating merely that the specimens were unfed. I have seen similar approximations in unfed larvae of *Erythraeus reginae* and *E. urrbrae*.

The systematic position of this species will be dealt with in a subsequent paper by Womersley.

Genus *CALLIDOSOMA* Womersley 1936.

*J. Linn. Soc. Lond., Zool., 40(269): 120.*

*Genotype: Caeculisoma ripicola* Womersley 1934 (adult).

*Generic Definition of Larva:* Eyes one on each side. Dorsal scutum squarish, with rounded angles, concave anteriorly; with 2 pairs of sensillary setae and 3 pairs of non-sensillary setae. Anterior sensillae at one-fourth the length of the shield back from the anterior margin; posterior sensillae on posterior margin of scutum. Anterior non-sensillary setae arise at anterolateral angles of scutum. Venter: 2 setae between coxae I, 2 between coxae II, 2 more between or just anterior to coxae III. Coxa I with one seta, coxae II and III each with 2 setae. Legs of 6 segments: coxa, trochanter, femur (with a pseudo-articulation), tibia, metatarsus, tarsus. Tarsus with a strong falciform empodium, over-reaching the 2 claws; anterior claw strong, falciform, simple; posterior claw pulvilliform, ciliated ventrally, and with a strong terminal hook. Palpal coxa, femur, genu, tibia, tarsus with 0, 1, 1, 3, 7 setae respectively; tibial claw strong, bifurcate. Mandibles rounded. Capitulum ventrally with 2 pairs of hypostomal setae.

*Remarks:* This definition is based on the larva of *Callidosoma womersleyi*, n. sp., only. Had not this larva been bred to a nymph, it would have been necessary to have provisionally included it in the larval genus *Erythraeus* Oudemans 1912 (non *Erythraeus* Latreille 1806).

*CALLIDOSOMA WOMERSLEYI*, n. sp. Figs. 22, A-K; 23, A-M.

*Description of Adult (Type).* Fig. 22, A-E: Red. Body ovoid, 830 $\mu$  long by 660 $\mu$  wide. Crista linear, continued beyond posterior sensillary area. Anterior end of crista bulbous. Distance between centres of anterior and posterior sensillae 243 $\mu$ . Sensillary setae to crista filiform, with a few ciliations, anterior 43 $\mu$  long, posterior 49 $\mu$ . Anterior sensillary area also carries 5 stout setae to 64 $\mu$  long, with broad pointed scales. Dorsal setae parallel-sided or slightly clavate, with the same broad, flattened, pointed scales, setae 32-58 $\mu$  long. Ventral setae fine, tapering, ciliated, 32-34 $\mu$  long. Palp as figured, claw ventrally with a broad blunt basal tooth. Legs stout: I 1280 $\mu$  long, II 860 $\mu$ , III 980 $\mu$ , IV 1280 $\mu$  (including coxae and claws). Tarsus I 180 $\mu$  long by 70 $\mu$  high. Metatarsus I 220 $\mu$  long. All metatarsi with the normal protuberances (smaller similar structures are present dorsally at the distal ends of the femora and tibiae).

*Description of Larva.* Fig. 23, A-M: Red. Body oval, 370 $\mu$  long by 240 $\mu$  wide. Dorsal scutum squarish, with convex sides and rounded angles, except for the slightly concave anterior margin; length 73 $\mu$ , width 83 $\mu$ . Shield with 2 pairs of sensillary setae, filiform, slightly ciliated, anterior 27 $\mu$  long, posterior 25 $\mu$ ; with 3 pairs of strong blunted ciliated non-sensillary setae, anterior 26 $\mu$  long, middle 25 $\mu$ , posterior 22 $\mu$ . Eyes 1+1, posterior and lateral to the shield. Dorsal setae fairly stout, with scales as figured, 21-36 $\mu$  long. Ventral setae almost spiniform with little ciliation, one pair between each pair of coxae. Behind coxae III setae arranged in rows of 4. Coxal setae: on I pointed, very slightly ciliated, 21 $\mu$  long; on II similar, 20 $\mu$ ; on III similar, 20 $\mu$ . Legs: I 510 $\mu$  long, II 505 $\mu$ , III 600 $\mu$  (including coxae and claws). Tarsal setae ciliated except for a long spiniform dorsal rod; empodium long, fairly strong, falciform, simple, over-reaching the 2 claws; anterior claw strong, falciform, simple; posterior claw pulvilliform, with a strong terminal claw. Capitulum as figured. Palpal femur, genu, tibia, tarsus with 1, 1, 3, 7 setae respectively. Palpal claw bifurcate.

*Description of Post-Larval Pupa (Pupa I).* Fig. 22, F: Red. Ovoid, flattened ventrally. Length 0.7 mm.; width 0.5 mm. Heavily setose; setae lanceolate, simple, to 105 $\mu$  long.

*Description of Nymph.* Fig. 22, G-K: Red. Body oval, 690 $\mu$  long by 475 $\mu$  wide. Crista and eyes as in adult, except that the anterior bulb of the crista carries only 2-3 non-

sensillary setae. Anterior sensillary setae  $45\mu$  long, posterior  $47\mu$ . Dorsal setae similar to adult, but weaker,  $30-50\mu$  long. Palp as figured; palpal claw ventrally with a broad blunt basal tooth. Legs: I  $1110\mu$  long, II  $810\mu$ , III  $890\mu$ , IV  $1180\mu$  (all including coxae and claws). Protuberances on legs as in adult. Tarsus I  $159\mu$  long by  $68\mu$  high. Metatarsus I  $192\mu$  long.

*Locality:* Glen Osmond, South Australia. Type adult (ACA 31) obtained by sweeping foliage of *Eucalyptus rostrata*, 19th Dec., 1936 (R.V.S.).

Larvae have been taken in fair numbers, attached to jassids, by sweeping the foliage of *Eucalyptus rostrata*, during December-February (mostly December) at Glen Osmond

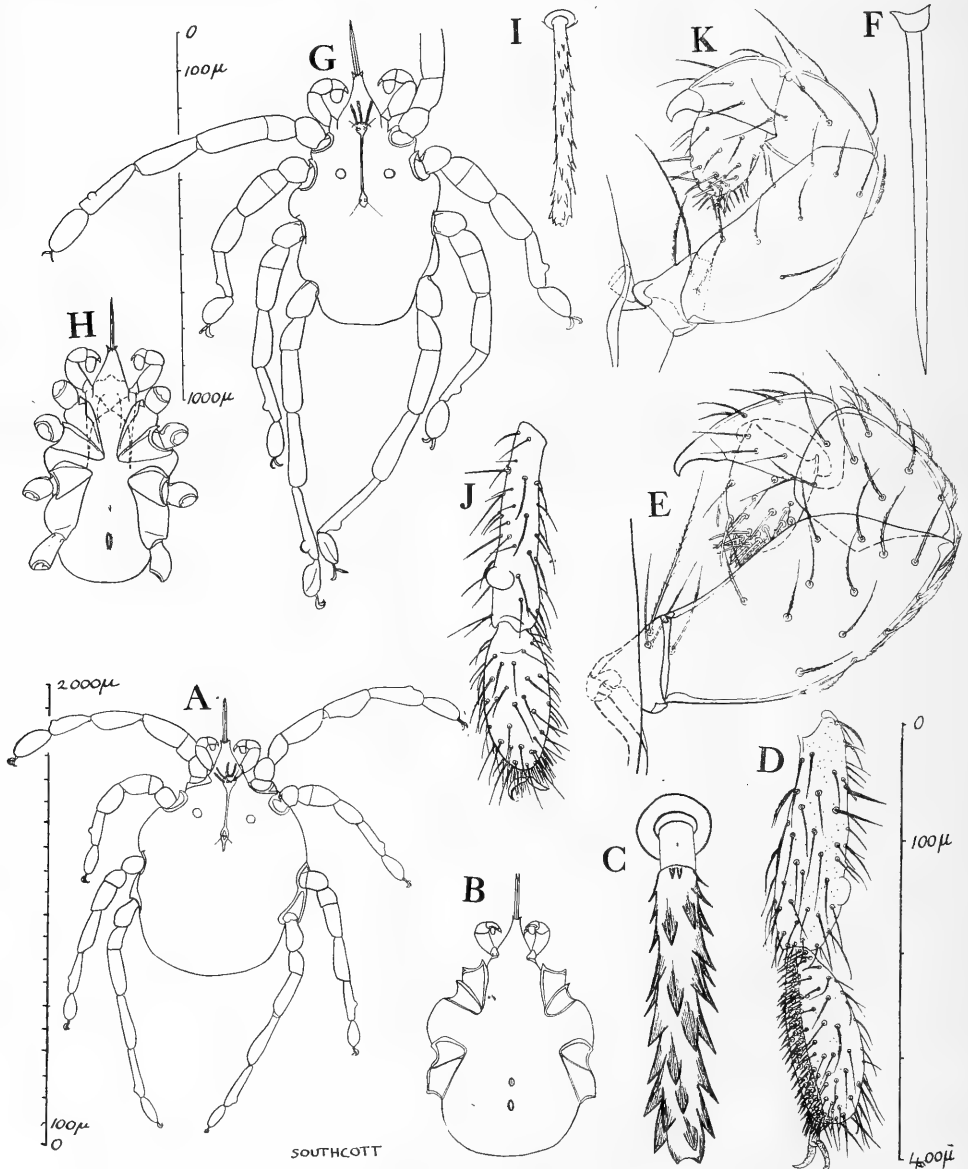


Fig. 22.—*Callidosoma womersleyi*, n. sp. A-D, Adult (type); A, Dorsal, outline; B, Venter, outline, to same scale; C, Dorsal seta; D, Tarsus I and metatarsus I; E, Palp; F, Pupa I, seta; G-K, Nymph; G, Dorsal, outline; H, Venter, to same scale; I, Dorsal seta; J, Tarsus I and metatarsus I; K, Palp. (I and C are to different scales.)

(1936-1939; R.V.S.). The larvae are attached to the abdomens of the jassids, underneath the wings (*not* on exposed parts; contrast *Erythraeus* spp. larvae). Frequently 2 or 3 larvae are on the one host.

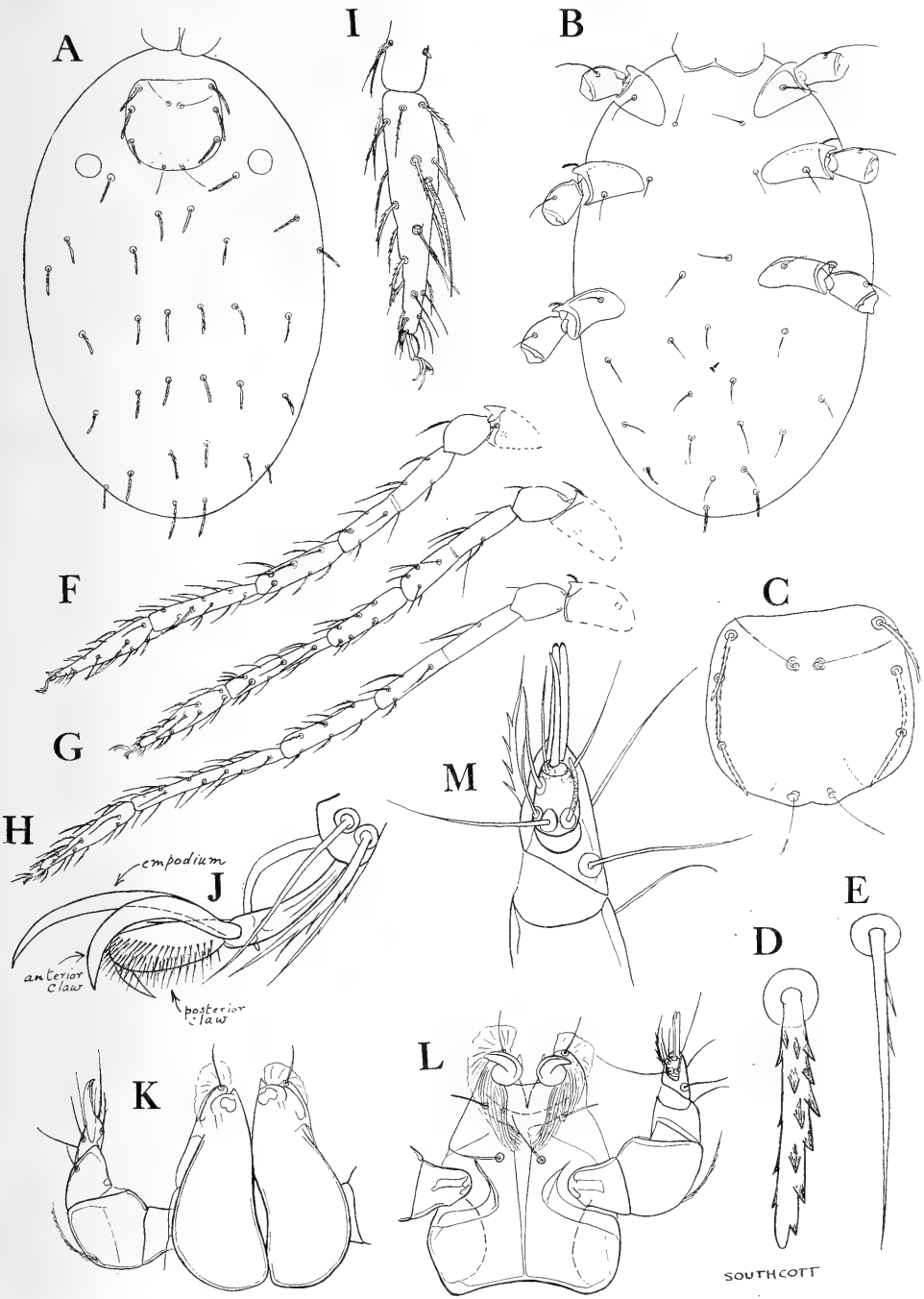


Fig. 23.—*Callidosoma womersleyi*, n. sp. Larva. A, Dorsum; B, Venter; C, Dorsal scutum; D, Dorsal seta; E, Ventral seta; F, G, H, Legs I, II, III (from above); I, Tarsus I; J, Tip of tarsus I; K, Capitulum from above, slightly distorted; L, Capitulum from below.

*Biology.*

Three specimens have been reared from larvae to nymphs, which have been correlated, on morphological grounds, with the adult obtained in the same locality. Relevant details are set out below:

Specimen.	ACA 24.	ACA 75.	ACA 140.
Larva detached from host	14.xii.36	25.xii.36	8.i.37
Became immobile . . . .	15.xii.36	27.xii.36	11.i.37
Ecdysis to Pupa I . . . .	19.xii.36	29.xii.36	—
Nymph emerged . . . . .	28.xii.36	10.i.37	23-27.i.37

Thus the pupa I stage lasts 9-12 days.

Genus *MICROSMARIS* Hirst 1926.

*Ann. Mag. nat. Hist.*, (9)18(108): 613.

*Belaustium* Womersley 1934 (as larva), *Rec. S. Aust. Mus.*, 5(2): 250.

[non] *Balaustium* von Heyden 1826 (adult), *Vers. syst. Einth.* in *Isis*, 20: 609. (See Oudemans, 1937, *Krit. Hist. Overz. d. Ac.*, III D, p. 1932.

*Genotype*: *Microsmaris mirandus* Hirst. *Ibid.*, p. 613.

*MICROSMARIS* sp. Fig. 24, A-E.

In 1934 Womersley described *Belaustium cristatum* (l.c., p. 251) from Glen Osmond, South Australia, as a common larval species there. It was allotted to *Belaustium* (*sic*) following Oudemans (1912). Similar or identical larvae have been taken at Glen Osmond by the author, from 1936 to 1940. They are found in vast numbers in the summer, running up trunks of eucalypts, and among the surrounding vegetation. As their numbers decrease in November and December the numbers of small nymphs of *Microsmaris* increase rapidly. These nymphs are identical in coloration with the larvae, and to the naked eye the mode of progression of the two is almost indistinguishable; in fact it needs close attention to distinguish them macroscopically in the field. On account of these details the author believed, as early as 1936, that these larvae belonged to the adult genus *Microsmaris*. Many attempts at rearing these larvae were made, small insects and water being provided, from 1936 onward. None of these was successful, nor was any larva ever taken by the author attached to an insect in the field. It was not until 1940 that the author was able to prove the relation between them. This was achieved by selecting in the field a number of the largest larvae available, and then confining them to tubes. Small insects were given, but these were not utilized; water and a piece of grass were also added to the tubes. From these experiments one larva (ACA 882B) from Glen Osmond was reared to a nymph. It became immobile on 19th Nov., 1940, pupated on 25th Nov., 1940, and a *Microsmaris* nymph emerged on 4th Dec., 1940, i.e., a first pupal instar of 9 days. This pupa is figured in Fig. 24, B-E.

At present it has not been possible to revise the taxonomy of the genus *Microsmaris*. It is worthy of remark that *Microsmaris goannae* Hirst 1928 (adult) was originally described from a neighbouring locality as a common species. Womersley's larva is here provisionally renamed *Microsmaris cristatus*. It is quite possible that Oudemans' larval "*Belaustium*" does really belong to the adult genus *Balaustium*. Whereas *Balaustium* is a world-wide genus, so far *Microsmaris* has been recorded from only Australia and New Zealand. *Balaustium* (adult) and *Microsmaris* (adult) appear to be fairly closely related. Adult specimens of *Microsmaris* from the same situation have laid small red eggs in captivity, but so far none of these has hatched.

## SUMMARY.

Experimental rearings of several genera and a number of species of Australian Erythraeidae have been accomplished, thus enabling a number of mistakes in the correlation of adult and larval genera to be rectified. The only Australian larvae of

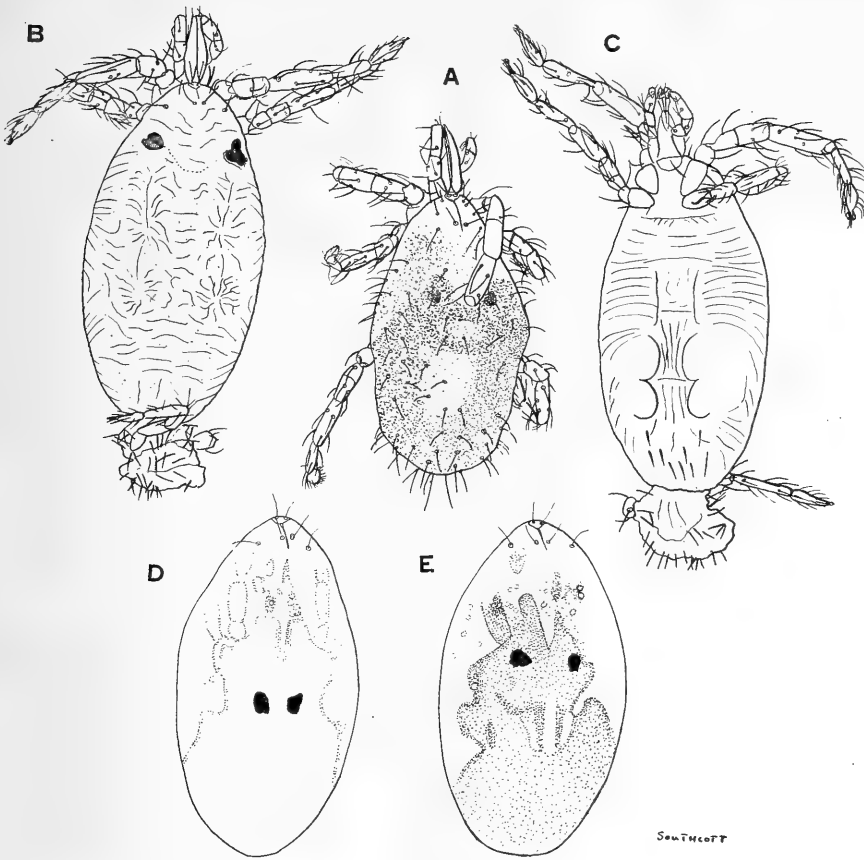


Fig. 24.—*Microsmaris* sp. A, Larva, fully-fed and immobile, prior to ecdysis, by transmitted light; B, Pupa I, with cast larval skin still attached, dorsal aspect (ACA 882B); C, Same from below; D, Same, showing outline of developing nymph, on 28.xi.40; E, Same on 1.xii.40.

Erythraeidae that were previously correctly generically correlated with adults belong to the genus *Leptus* Latreille 1796. *Erythraeus* larval is a heterogeneous group with no relationship to the adult genus *Erythraeus* Latr. 1806. The larva of *Callidosoma* Womersley 1936 is described; but for the successful rearing of larvae to nymphs, it would have been necessary provisionally to include the larva of this species in *Erythraeus* larval. The larval genus *Bochartia* Oudemans 1910 has been proven to be the larva of *Erythraeus* Latr. 1806 by the successful rearings of a number of species. Womersley's larval *Belaustum cristatum* has been proven to belong to the adult genus *Microsmaris* Hirst 1926.

Two species of erythraeid mites have been successfully reared through every stage of their life-histories, thus enabling the life-history of the Erythraeidae to be defined: egg (5–11 months), larva (1–3 weeks), pupa I (9–16 days), nymph (21–39 days), pupa II (15–16 days), adult (several weeks and longer). The cycle occurs annually, the major portion of the life-history being passed as the egg. No such rearing has previously been accomplished in this family.

The taxonomy of part of the Australian Erythraeidae has been revised, 3 new genera being erected: *Erythroides*, n. gen. for *Erythraeus serratus* Womersley 1936, and 3 new species described, also a larva proven to belong to this genus by an experimental rearing, and thus enabling the larval characters for the genus to be defined; *Erythrellus*, n. gen. and *Parerythraeus*, n. gen. for entirely new forms.

The taxonomic revision covered in this paper is set out thus:

Adult.	Larva, etc.
<i>Erythrellus imbricatus</i> , n. gen., n. sp.	Not known.
<i>Parerythraeus gregoryi</i> , n. gen., n. sp.	Not known.
<i>Erythroides</i> , n. gen.	Larva defined; previously unknown.
<i>Erythroides serratus</i> .	?
= <i>Erythraeus serratus</i> Wom. 1936.	
<i>Erythroides neoserratus</i> , n. sp.	?
?	<i>Erythroides clavatus</i> , n. sp.
<i>Erythroides darwini</i> , n. sp.	Not known.
<i>Erythroides macdonnelli</i> , n. sp.	Not known.
<i>Erythraeus</i> Latr. 1806.	<i>Bochartia</i> Ouds. 1910.
<i>E. celeripes</i> (Rainbow 1906).	Not known.
<i>E. imperator</i> (Hirst 1928).	Probably <i>E. oudemansi</i>
	= <i>Bochartia oudemansi</i> Wom. 1936.
<i>E. reginae</i> (Hirst 1928).	Larva previously unknown; described; also every other stage in the life-history.
<i>E. antepodians</i> (Hirst 1928).	Not known.
Not known.	<i>E. stuarti</i> , n. sp.
<i>E. guttatus</i> , n. sp.	Probably <i>E. osmondensis</i> , n. sp.
<i>E. pilosus</i> (Hirst 1928).	Larva and pupa I and nymph described; previously unknown.
<i>E. urbrae</i> Wom. 1934.	Every stage in life-history reared, described. Larva previously described as <i>Bochartia</i> ? <i>longipes</i> Wom. 1934.
Not known.	<i>E. womersleyi</i> , n. sp.
<i>Leptus</i> Latr. 1796.	Previously correctly correlated. Confirmed by the rearing of a larva to a nymph (not described in text).
Not known.	<i>Leptus anomalus</i> , n. sp.
<i>Callidosoma</i> Wom. 1936.	Larva established; previously unknown.
<i>C. womersleyi</i> , n. sp.	Larva, pupa I, nymph described; previously unknown.
<i>Microsmaris</i> Hirst 1926.	See below.
Possibly <i>M. goannae</i> Hirst 1928.	Larva <i>Belaustium cristatum</i> Wom. 1934 proven as <i>Microsmaris</i> ; pupa I figured.

#### ACKNOWLEDGEMENTS.

Sincere thanks are due to Mr. H. Womersley for advice and encouragement, and to him and to the Director of the South Australian Museum for the opportunity of examining Womersley's type material, and also that of Rainbow and Hirst.

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POLLENS OF *NOTHOFAGUS* BLUME FROM TERTIARY DEPOSITS IN AUSTRALIA.

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(Communicated by Dr. Ida A. Brown.)

(Plates i-ii; eleven Text-figures.)

[Read 24th April, 1946.]

INTRODUCTION.

In view of the general recognition that fossil pollens, when studied in conjunction with pollens of living species, provide reliable information regarding the composition and distribution of past floras, it is surprising that in Australia this field has, hitherto, been unexplored.

Tertiary palaeobotanists in this country have largely restricted themselves to the macroscopical study of leaf impressions many of which are of a fragmentary and doubtful nature. Pollen grains are generally conceded to be less variable units than leaves, so that a study of fossil pollens should both widen our conception of Australian floras and throw light on the origins of endemic species. For these reasons an investigation covering the pollen content of Australian Tertiary and Recent deposits has been planned.

Practically no literature exists that deals specifically with pollens of living Australian plants; and, although Cranwell's (1939, 1940, 1942) excellent memoirs on New Zealand pollens are extremely helpful in the elucidation of species common to both countries, the identification of fossil species will, necessarily, be slow, and some considerable time must elapse before any generalizations can be made. In the meantime, it is proposed to publish at intervals illustrated botanical descriptions whereby the genera present in the various geological deposits may be recognized, also the bases upon which these identifications have been made.

Since pollens of *Nothofagus* spp. are amongst the most conspicuous that have been isolated, both numerically and specifically, they have been selected as the subject of this introductory paper. They occur more or less abundantly in the majority of lignites, clays and mudstones that have been examined at present. Moreover, their characteristics are so distinctive that no question of generic identity arises and the unmodified name *Nothofagus* can be used with confidence. Several clearly defined kinds are preserved. These are regarded as pollens of individual fossil species, but instead of providing them with specific names, they will subsequently be referred to as *Nothofagus* sp. with a different letter of the alphabet to designate each.

Nine species of *Nothofagus* have already been distinguished in Australian Tertiary rocks by variation in leaf-form. Nevertheless, until organic connection between recognizable leaves and male flowers with pollen *in situ* is established, identification of the pollen types with any of these species will be impossible.

The distribution of the fossil species will be indicated; but it has not been possible to consider this at all exhaustively. It must remain for future work, also, to trace the vertical range of individual types through any one deposit.

SOURCE AND AGE OF SAMPLES INVESTIGATED.

*Lignites and Ligneous Clays.*

The extensive seams of brown coal and associated ligneous clays that occur in southern Victoria and south-eastern South Australia have provided the major source of the fossil beech pollens to be described below. These deposits reach a maximum thickness, probably exceeding 1,000 feet, in the Latrobe Valley in south-eastern Victoria where

at Yallourn and Morwell they are being worked by the State Electricity Commission. Boring operations at present in progress have, through the courtesy of the staff of the Commission, facilitated the examination of samples from specified levels. The following localities will be referred to in connection with the distribution of fossil pollens (Text-fig. 1).



Text-fig. 1.—Map of south-eastern Australia showing location of deposits in which *Nothofagus* spp. occur. (Prepared by the Geological Survey of Victoria.)

(a) *Victoria.*

Altona. Lignite from Melbourne and Altona Colliery Company's mine at 362 feet level No. 9 dip. G.S.V.\* specimen.

Parwan. G.S.V. Bores 9 and 10, about 30 miles west of Melbourne.

Lal Lal. Samples from dump of an abandoned mine 15 miles south-east of Ballarat.

Beenak. (Kemble, 1925.) Lignite from allotment 68c, Parish of Beenak, about 6½ miles from Yarra Junction. M.U.G.D.† specimen.

Boolara. Lignite from Mirboo Colliery shaft at the 162 feet level, 3 miles north-east of Boolara. G.S.V. specimen.

Budgerec. Lignite from shaft in allotment 6D, Parish of Budgerec. G.S.V. specimen.

Korumburra south of Parish of Leongatha, ligneous clay from Bore at 350 feet. G.S.V. specimen.

Maryvale. Ligneous clay from Bore 155 at 552 and 760–761 feet.

\* G.S.V., Geological Survey of Victoria.

† M.U.G.D., Melbourne University Geological Department.



Maryvale. Lignite from Bore 169, 392-402 feet.

Yallourn. Lignite from open cut, S.E.C. samples 1-6 taken at depths from top of coal of 11, 32, 62, 92, 120, 150 feet respectively.

Yallourn. Ligneous clay from floor of open cut. M.U.G.D. specimen collected by Professor E. S. Hills.

(b) *South Australia.*

In this State the chief brown coal deposits are situated near Moorlands, a railway station on the Pinaroo line about 87 miles south-east of Adelaide (Mawson and Chapman, 1922). Preparations were made from a mixed coal-sample obtained from the Mines Department of South Australia.

(c) *New South Wales.*

Samples from the Southern Tableland were provided by Dr. J. A. Dulhunty from his coal collection as follows:

Kiandra, New Chum Hill (Sussmilch, 1937, p. xii). C.S. 104, ligneous clay, 30 feet below the base of the basalt. C.S. 87, low grade coal, 70 feet below the basalt. C.S. 103, soft ligneous shale 135 feet below the basalt.

Berridale, Wullwye Creek, C.S. 89, ligneous clay over 100 feet below the basalt.

*Sandstones, Mudstones, etc.*

Anglesea (Singleton, 1941, p. 24). Black carbonaceous sandstone from cliffs 1 mile north-east of mouth of Anglesea River, Parish of Jan Juc, Victoria.

Balcombe Bay (Singleton, 1941, p. 26). Mudstone containing leaf-remains from coastal cliffs about 2 miles south of Mornington, Victoria.

Vegetable Creek (Emmaville) (Sussmilch, 1937, p. ix). Mudstone from deep leads in the New England Tableland, northern New South Wales. M.U.G.D. Fossil Collection, Nos. 242, 501.

Unanimity of opinion regarding the detailed stratigraphy of the Tertiary rocks of south-eastern Australia has not yet been reached. Somewhat different views are held by the chief workers. Singleton (1941, p. 49) suggests Oligocene as the probable age of the brown coal deposits, while Crespin (1943) places them as Lower to Upper-Middle-Miocene. Singleton also tentatively assigns the Anglesea sandstones and the leads of the Vegetable Creek to the Oligocene Epoch.

In view of this position, it appears that Oligocene-Miocene is the closest approximation to the age of the fossil *Nothofagus* pollens possible at present.

TREATMENT OF MATERIAL.

The method that has proved most satisfactory for the making of pollen preparations from Tertiary lignites is the chlorination-acetolysis method devised and perfected by Erdtman (1943, p. 34). The ease, however, with which the extraneous material is removed from individual samples has been found to vary considerably with the nature of the coal itself. Usually it is necessary to give the acetolysed residue one or even several washings with warm caustic potash of strengths ranging from 0.5-10% according to its resistance to clearing.

After a preliminary treatment with hydrofluoric acid the same method has been employed in the examination of sandstones, mudstones and ligneous clays. When, as sometimes happens, a lignite contains a certain amount of silica, more satisfactory preparations are obtained if treatment with hydrofluoric acid precedes acetolysis.

Glycerine-jelly has been employed exclusively as a mounting medium, either uncoloured or coloured lightly with basic fuchsin.

INVESTIGATIONS ON *NOTHOFAGUS* POLLENS.

*Nothofagus* pollen was first described in 1929 by von Post (1929), who based his description on three living South American species.

In 1933 Auer recorded and figured *Nothofagus* pollens from peats of Tierra del Fuego, without, however, giving detailed information regarding their salient features. Cranwell and von Post (1936) recognized the distinction between *N. Menziesii* pollen

and the pollens of the other four New Zealand species and recorded the presence of both types in post-Pleistocene peats.

It remained for Cranwell (1939) to describe in detail the pollens of most of the living species. By means of these descriptions the identification of southern beech pollens in peats and the determination of the affinity of older types are now possible. The separation of *Nothofagus* species into two pollen-groups, named by Cranwell the *Menziesii* and *fusca* groups respectively, is an interesting and important basis for work on fossil species. Cranwell found that most of the New Zealand and South American species have pollen of the *fusca* type whereas two of the three Australian species have pollen of the *Menziesii* type. Records of *N. Menziesii* and *N. fusca* pollens from various New Zealand peats were made. In addition, the *fusca* type was recorded from a Tertiary deposit at Kaikorai, and a possible "intermediate type" from Whangamarino was briefly described.

A description of the pollen of the Tasmanian species, *N. Gunnii* (Hook.) Oerst was not included in Cranwell's paper. In a separate note\* I have shown this pollen to be of the *fusca* type.

#### IDENTIFICATION OF NOTHOFAGUS POLLENS.

As the result of comparisons made between the pollens of wind-pollinated members of the Fagaceae, namely, *Quercus*, *Fagus* and *Nothofagus*, Cranwell (1939) was able to arrive at a "basic description" to cover all three types. This is quoted as follows: "Grains rather large, usually about .040 mm. more or less spherical to very flattened; furrows wherever recognizable directed meridionally, the pores where present being arranged in an equatorial circle. Exine fairly thick, always warty-granular."

*Fagus* and *Quercus* pollens have three furrows; *Nothofagus* pollens on the other hand have several, which are usually coincident with the pores. *Nothofagus* pollens of Cranwell's *Menziesii* group (Plate i, fig. 1) have diameters of from 40–60 $\mu$ , a thin exine, and in place of functional pores for the emergence of the pollen-tubes, fissure-points around the equator where rupturing of the grains takes place. *Nothofagus* pollens of the *fusca* type (Plate i, fig. 16) are usually less than 40 $\mu$  and the exine is thick, especially around the pores.

The fossil types all conform to the basic description given above. Most of them have well-defined meridionally placed pores or furrows which apparently were functional, and prominent sculpture. The characters that have been relied upon to distinguish the various forms have been pore-number, thickness of exine, type of sculpture, and, less frequently, size of grain. Wherever possible the pore-number and average size have been determined from a large number of individual counts, in some instances amounting to several hundreds. In no case has a value used been derived from less than 50 grains.

The decision to allow a wide size-range within a type is supported by the existence of this feature in the pollen of some of the living species, for example, *N. Menziesii* in which Cranwell noted a difference of 20 $\mu$  between the smallest and largest grains.

Variation in the strength of the sculpture also occurs. This has raised difficulties in the matching of types in preparations from different localities. A broad view of these divergencies has been adopted. It is recognized that later, when individual deposits are worked at regular vertical intervals, further subdivision of some of the fossil species may be necessary. This is particularly so, for instance, with the Moorlands lignite, in which, judging from the mixed sample examined, some of the beech pollen-types are difficult to match exactly with those from more eastern localities.

In connection with the occurrence of such variations as quality of sculpture and average size within the fossil species described in this paper, it must be borne in mind that evidence of hybridization between members of the *fusca* pollen group has been established for New Zealand species (Anonymous, 1944) and that this has an effect on certain characters of the pollen of the hybrid (Cranwell, 1939). Since crossing is occurring naturally at the present time, there is reason to think that it may have taken

\* "Note on the Pollen of *Notofagus Gunnii* (Hook.) Oerst." To be published in *Proc. Roy. Soc. Vict.*, 58 (1), 1946, p. 1.

place during the past history of the genus and that some of the difficulties experienced in placing, systematically, what appear to be atypical pollens may be due to this cause.

DESCRIPTIONS OF FOSSIL POLLENS.

*Nothofagus* sp. a. (Plate i, figs. 5-7. Text-fig. 2. Table 1).

*General remarks.*—Conforms closely to the description of *N. Menziesii* given by Cranwell (1939, p. 182) and can be distinguished readily from other *Nothofagus* pollens in the samples examined on account of its size, delicate exine, and the absence of either furrows or pores.

*Grain.*—Large, diameter 40-60 $\mu$  with an average of 52 $\mu$ . When unruptured, circular or slightly angular with the positions of the fissure-points faintly indicated around the equator. The majority of grains are, however, much flattened and partially or completely ruptured, when their outline becomes strongly angular. The fissures range from 6-9, the commonest number being 7, and gape widely.

*Exine.*—Less than 1 $\mu$  and completely covered with small sharply-pointed papillae.

*Affinity.*—A close affinity exists between *N. sp. a.* and pollens of the *Menziesii* type; these pollens, owing to their strikingly uniform character, are extremely difficult to distinguish from one another. All have 7 as the predominant number of fissure-points, and should they occur together in a pollen mixture, the sculpture is hardly sufficiently distinctive to allow of confident specific identification.

Acetolysed pollens of *N. Menziesii* Oerst, *N. Moorei* (F. Muell.) Maiden and *N. Cunninghamsi* (Hook.) Oerst\* have been carefully studied in conjunction with those of *N. sp. a.*, and so that direct comparisons can be made, photographic illustrations of them are provided in Plate i, figs. 1-4.

Although the fossil grain has a slightly greater diameter and wider size-range, it is very close to the pollen of *N. Moorei*, the papillae in both tending to be slightly less crowded than in either *N. Menziesii* or *N. Cunninghamsi*. In this connection it is interesting to note that von Ettingshausen (1888, p. 34) observed a remarkable resemblance between the leaves of his species, *Fagus Wilkinsoni*, *Nothofagus Wilkinsoni* (Ett.) Paterson (1934) and those of *N. Moorei*, and went so far as to say: "The supposition that there is a genetic connection between the two species, cannot therefore be wrong."

In the absence of macroscopical remains in intimate association with *N. sp. a.*, its identification with any one of the recognized species of *Nothofagus*, either living or extinct, would be unsound; but the evidence is clear that pollen of the *Menziesii* type had evolved by the Miocene Epoch, and that the species producing it was fairly widely distributed.

*Distribution.*

*Lignites:* Beenak.

*Ligneous Clay:* Maryvale Bore 155, 552 feet level; south of Korumburra Bore 5 at 570 feet.

*Ligneous Shale:* Kiandra C.S. 103.

*Mudstones:* Balcombe Bay, Vegetable Creek.

TABLE 1.

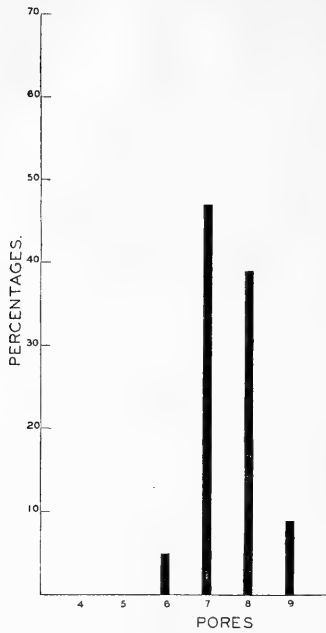
Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Maryvale Bore 155, 552 feet ..	42.5-63.8 $\mu$	53 $\mu$	6-9	49% 7
Vegetable Creek .. ..	40.0-63.8 $\mu$	52 $\mu$	6-9	49% 7

*Nothofagus* sp. b. (Plate i, figs. 8-13. Text-fig. 3. Table 2).

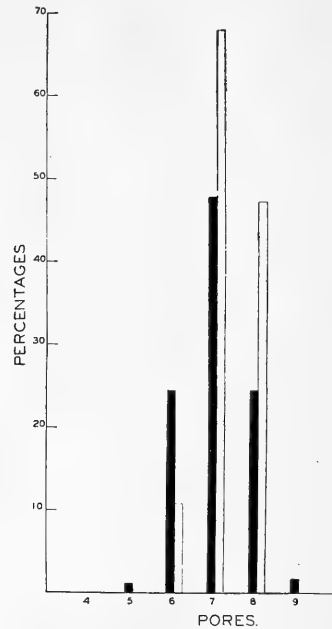
*General remarks.*—A pollen that conforms to the general description of *N. fusca* (Cranwell, 1939, p. 185).

*Grain.*—Bi-convex, typically circular in polar view. Size-range 21.5-40.0 $\mu$ , the collective average from all localities being 30 $\mu$ . Pores 5-9, mainly 6 and 7, the majority 7; sunken about 2.5 $\mu$ .

\* Pollen of *N. obliqua* (Mirb.) Blume, the South American member of this group, has not been available for comparison.



Text-fig. 2.



Text-fig. 3.

Text-fig. 2.—Pore-frequencies in *N. sp. a.* from Maryvale. Bore 155 at 552 feet.

Text-fig. 3.—Pore-frequencies in *N. sp. b.* □ Maryvale. Bore 155 at 762 feet; ■ Vegetable Creek.

*Exine*.—Firm, about  $1.3\mu$  thick between the pores,  $2.0$ – $2.6\mu$  at the rims of the pores. Sculpture strong and clear, papillae very short and moderately close.

*Affinity*.—Characters such as the collar-like pore-rims and the type of sculpture place *N. sp. b.* unquestionably in the *fusca* group and completely demonstrate that the second of the two divergent pollen groups was also well established during Miocene times.

The existing species with which it is most natural that *N. sp. b.* should be compared is *N. Gunnii*, which alone of the living Australian species has pollen of the *fusca* type (Plate i, figs. 14, 15). Undoubtedly close agreement exists between these two pollens, their average sizes are practically identical and the fact that the majority of grains have 6 or 7 pores is noteworthy. The pore-maxima, however, are different. In *N. Gunnii* the majority of grains have 6 pores, whereas in *N. sp. b.* the maximum falls on 7. Moreover, the sculpture of the latter is stronger and the exine slightly thinner.

In view of the fact that the majority of New Zealand and South American beeches have pollen of the *fusca* type, it is tempting to speculate upon the connection between these and the Australian species with the same variety of pollen. Unfortunately, considerably more information is needed from peats and deep deposits in those countries, as well as in Australia, before this interesting evolutionary and phytogeographical problem will be solved.

#### Distribution.

*Lignites*: Moorlands, Beenak, Boolara, Thorpdale.

*Ligneous Clays*: Maryvale Bore 155 at 552 and 762 feet levels.

*Sandstones and Mudstones*: Anglesea, Balcombe Bay, Vegetable Creek.

TABLE 2.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Anglesea .. .. .	21.0-34.6 $\mu$	27.0 $\mu$	5-8	54.5% 7
Maryvale Bore 155, 762 feet	26.6-37.0 $\mu$	30.6 $\mu$	6-8	68.0% 7
Moorlands .. .. .	26.6-40.0 $\mu$	32.0 $\mu$	6-8	61.0% 7
Vegetable Creek .. .	26.6-40.0 $\mu$	32.0 $\mu$	5-9	47.0% 7
Maryvale Bore 155, 552 feet	26.6-40.0 $\mu$	33.0 $\mu$	5-8	57.5% 7

*Nothofagus* sp. c. (Plate i, figs. 17, 18. Text-fig. 4. Table 3).

*General remarks.*—A clearly defined extinct pollen of the *fusca* type, from present experience, usually preserved in comparatively small numbers. Most abundant in samples from Lal Lal and Vegetable Creek.

*Grain.*—Delicate, flattened, frequently folded or wrinkled, circular in polar view. Large, size-range 26.6–64.0 $\mu$ , average approximately 40 $\mu$ . Pores 5–8, very rarely 4, mainly 6 and 7; sunken about 3 $\mu$ .

*Exine.*—Delicate, about 1 $\mu$ , 3–4 $\mu$  around the pores. Sculpture fine and often inconspicuous.

*Affinity.*—A further clear example of the *fusca* pollen-group. Not to be confused with either *N. sp. b.* or other pollens of this group on account of the delicate exine and contrastingly conspicuous pore-rims.

*Distribution.*

*Lignites:* Moorlands, Parwan Bores 9 and 10, Lal Lal, Beenak, Boolara, Thorpdale.

*Ligneous Clays:* Maryvale Bore 155 at 552 and 760 feet levels, Berridale C.S. 89.

*Sandstones and Shales:* Anglesea, Balcombe Bay, Vegetable Creek.

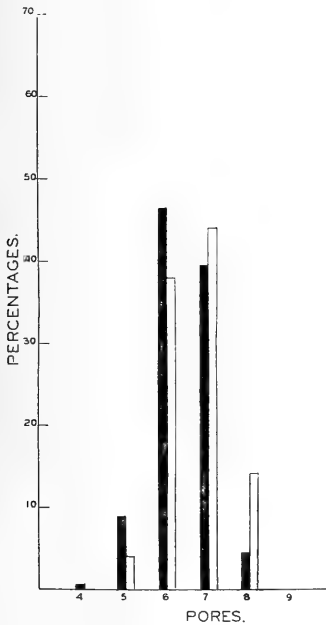
TABLE 3.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Lal Lal ..	26.6–53.0 $\mu$	37.5 $\mu$	4–8	46.5% 6
Vegetable Creek ..	29.5–64.0 $\mu$	45.0 $\mu$	5–8	44.0% 7

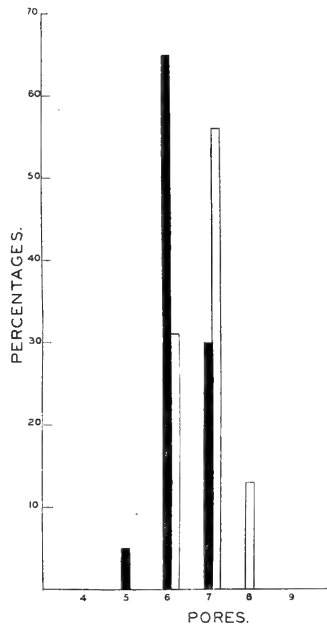
*Nothofagus* sp. d. (Plate i, figs. 19–21. Text-fig. 5. Table 4).

*General remarks.*—A widespread, characteristically small, echinate pollen.

*Grain.*—Bi-convex almost circular in polar views. Size-range 18.6–35.0 $\mu$ , the average size varying fairly considerably with the locality (Table 4). Pores 5–8, mainly 6 and 7, sunken approximately 2.5 $\mu$ .



Text-fig. 4.



Text-fig. 5.

Text-fig. 4.—Pore-frequencies in *N. sp. c.* □ Vegetable Creek; ■ Lal Lal.

Text-fig. 5.—Pore-frequencies in *N. sp. d.* □ Parwan Bores 9 and 10; ■ Yallourn open cut, 62-150 feet.

*Exine*.—Firm, 1–2 $\mu$  conspicuously thickened around the pores. Sculpture prominent in proportion to the size of the grain, in the form of clear echinate papillae about 1.0–1.5 $\mu$  in length and from approximately 0.5–2.0 $\mu$  across the base.

*Affinity*.—The thickening of the exine around the pores at once suggests a resemblance to the pollen of the *N. fusca* type, but the sculpture is markedly different and the sharply pointed papillae recall those of the *N. Menziesii* pollen group. *N. sp. d.* appears to be a clear example of an intermediate type.

*Distribution*.

*Lignites*: Moorlands, Parwan Bores 9 and 10, Beenak, Yallourn open cut 62–150 feet, Maryvale Bore 174 at 40–50 feet, Budgeree, Thorpdale.

*Ligneous Clay*: Maryvale Bore 155 at 552 feet.

*Sandstones and Mudstones*: Anglesea, Balcombe Bay, Vegetable Creek.

TABLE 4.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Maryvale Bore 174, 40–50 feet	21.0–26.6 $\mu$	24.5 $\mu$	5–8	58% 6
Anglesea .. .. .	21.0–26.0 $\mu$	24.5 $\mu$	5–8	50% 7
Maryvale Bore 169, 392 feet	21.0–29.0 $\mu$	25.0 $\mu$	6–8	62% 7
Yallourn open cut, 62–150 feet	18.6–32.0 $\mu$	26.6 $\mu$	5–7	65% 6
Balcombe Bay .. .. .	24.0–29.0 $\mu$	27.0 $\mu$	6–8	68% 7
Moorlands .. .. .	26.6–35.0 $\mu$	29.0 $\mu$	6–8	67% 7

The types that follow represent pollens of extinct species of *Nothofagus*, none of which can be directly associated with the present-day pollen groups. The fact that the pore-slits were clearly defined and opened without rupture of the grain separates them from the *Menziesii* group. By the uniform thickness of the exine they are removed from the *fusca* group.

*Nothofagus sp. e.* (Plate ii, figs. 22–25. Text-fig. 6. Table 5).

*General remarks*.—The most widespread and abundant beech pollen in the deposits examined.

*Grain*.—Strongly angular in polar view due to the deeply-sunken pores. Size-range 18.6–42.5 $\mu$  with an exceedingly variable average over a range of localities (Table 5). Pores 4–7, mainly 5 and 6, the majority 6, sunken 5–8 $\mu$ .

*Exine*.—Thin but firm, of uniform thickness, approximately 1 $\mu$ , forming definite though unthickened rims to the pore-slits. Sculpture fine, sometimes faint; papillae short and pointed, frequently less crowded and smaller towards the equator.

*Affinity*.—Appears to be indicated with *N. sp. f.* in which there is a general similarity of form. In samples such as those from Balcombe Bay where *N. sp. e.* is associated with *N. sp. h.* some difficulty may be experienced in assigning grains with identical pore numbers to one or other species. When, however, large numbers of grains are carefully examined, the chief specific difference, that is, the lower pore-maximum and pore-range of *N. sp. e.*, becomes clear.

*Distribution*.

*Lignites*: Moorlands, Parwan Bores 9 and 10, Altona, Beenak, Yallourn open cut 62–150 feet, Maryvale Bore 169, 392 feet, Boolara, Thorpdale.

TABLE 5.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Maryvale Bore 169, 392 feet ..	21.0–29.0 $\mu$	24.0 $\mu$	4–7	58% 6
Yallourn clay .. .. .	18.6–40.0 $\mu$	29.0 $\mu$	4–7	51% 5
Thorpdale .. .. .	24.0–40.0 $\mu$	29.5 $\mu$	5–7	55% 6
Boolara .. .. .	26.6–40.0 $\mu$	30.5 $\mu$	5–7	68% 6
Balcombe Bay .. .. .	24.0–40.0 $\mu$	32.0 $\mu$	5–7	57% 6
Yallourn open cut S.4, 92 feet	21.0–42.5 $\mu$	33.0 $\mu$	4–7	48% 6

*Ligneous Clays*: Yallourn open cut S.4, 92 feet, Maryvale Bore 155, 552 feet, Kiandra C.S. 103, C.S. 104, Berridale, C.S. 89.

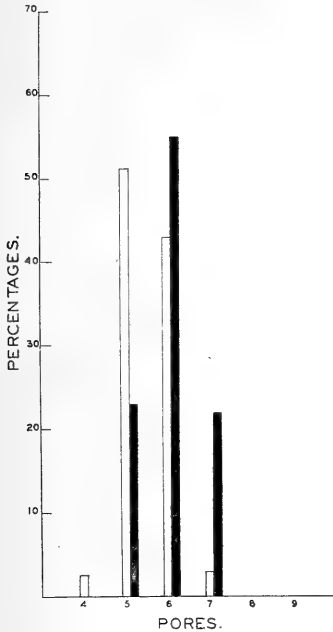
*Sandstones and Mudstones*: Anglesea, Balcombe Bay, Vegetable Creek.

*Nothofagus* sp. f. (Plate ii, figs. 26–29. Text-fig. 7. Table 6).

*General remarks*.—A uniform and widespread type. Present in smaller numbers than *N. sp. e.* with which it appears to be frequently associated.

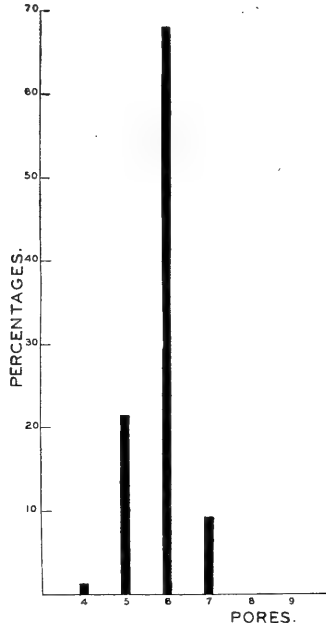
*Grain*.—Bi-convex and prominently angular in polar view with deeply set pores. Size-range from 26–47 $\mu$  with an average from several localities of approximately 34 $\mu$ . Pores 4–7, mainly 5 and 6, sunken from 5–7.5 $\mu$ .

*Exine*.—About 2 $\mu$ , usually thinning slightly towards the well-defined rims of the pore-slits and frequently embayed between them. Papillae clear, short, sharply-pointed, becoming slightly smaller towards the equator of the grain, typically rather widely spaced at intervals of 1.5–2.5 $\mu$ .



Text-fig. 6.

Text-fig. 6.—Pore-frequencies in *N. sp. e.* □ Yallourn clay; ■ Thorpdale.



Text-fig. 7.

Text-fig. 7.—Pore-frequencies in *N. sp. f.* from Boolara.

*Affinity*.—In its low pore-number, firm exine, deeply sunken pores and angular character, *N. sp. f.* closely approaches *N. sp. e.* It is treated as a separate species on account of the consistently thicker exine, the more distantly placed papillae and the frequent embayment of the exine between the rims of the pore-slits.

*Distribution.*

*Lignites*: Moorlands, Altona, Yallourn S.4, 92 feet, Boolara, Budgeree.

*Ligneous Clay*: Maryvale Bore 155 at 552 feet.

*Sandstones, Mudstones*: Anglesea, Balcombe Bay, Vegetable Creek.

TABLE 6.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Maryvale Bore 155. 552 feet	26.6–40.0 $\mu$	32.5 $\mu$	5–7	51% 6
Balcombe Bay .. ..	29.0–40.0 $\mu$	32.5 $\mu$	5–7	59% 6
Boolara .. .. .	26.6–40.0 $\mu$	33.0 $\mu$	4–7	68% 6
Vegetable Creek .. ..	26.6–42.5 $\mu$	33.0 $\mu$	5–7	60% 6
Moorlands .. .. .	31.0–47.0 $\mu$	40.0 $\mu$	4–7	55% 6

*Nothofagus* sp. *g.* (Plate ii, figs. 30-32. Text-fig. 8. Table 7).

*General remarks.*—One of the larger and rarer types, the limits of which are the least clearly defined. Present in sufficient numbers for critical analysis in preparations from only two localities, namely, Vegetable Creek and Beenak.

*Grain.*—Large, considerably flattened and strongly angular in polar view. Size-range 32.0-58.5 $\mu$ , the average being between 40-45 $\mu$  (Table 7). Pores 4-7, majority 5 and 6, sunken 8.0-10.5 $\mu$ .

*Exine.*—Delicate, approximately 1 $\mu$  or even less as in the examples from Vegetable Creek. Sculpture distinct, papillae fine, sharp, rather widely spaced at distances approximating to 2-3 $\mu$ .

*Affinity.*—This species is insufficiently known at present. All examples have been more or less fully expanded. On account of the delicate nature of the exine some difficulty was experienced in deciding whether the deep gaps, evident in every grain, represent fissures or widely open predetermined narrow-rimmed pore-slits related to functional pores. The latter view, adopted after careful examination of the Vegetable Creek form, has been confirmed by examples in preparations of lignite from Beenak. In these the exine is slightly thicker and the rims to the pore-slits more distinct.

In spite of the low pore-number, *N.* sp. *g.* approaches more closely than any of the other fossil species to pollens of the *Menziesii* group in general and to *N.* sp. *a.* in particular. It is possible that it may prove to be a stage in the evolutionary history of this pollen group.

*Distribution.*

*Lignites:* Moorlands, Beenak.

*Mudstones:* Vegetable Creek.

TABLE 7.

Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Vegetable Creek .. ..	34.5-58.5 $\mu$	45.5 $\mu$	4-6	51% 5
Beenak .. ..	32.0-50.5 $\mu$	40.0 $\mu$	5-7	54% 6

*Nothofagus* sp. *h.* (Plate ii, figs. 33-35. Text-fig. 9. Table 8).

*General remarks.*—This type has been observed in samples from only two localities. The following description is based, mainly, upon pollens obtained from the mudstones of the Balcombe Bay leaf-bed, in which it is particularly abundant.

*Grain.*—Rather flattened, somewhat angular in polar view. Size-range from 26.6-48.0 $\mu$ , the average being about 35 $\mu$ . Pores 6-9, mainly 7 and 8, majority 7, sunken approximately 5 $\mu$ .

*Exine.*—Thin but firm, about 1 $\mu$ , forming narrow rims to the pores. Sculpture fine, moderately dense, papillae short, pointed, coarser and closer at the poles.

*Affinity.*—As previously mentioned, 6- and 7-pored examples of *N.* sp. *h.* are often difficult to distinguish from grains of *N.* sp. *e.* with the same number of pores. The occurrence, in a sample, of thin-walled grains with decided pores in which the numbers 7 and 8 predominate would suggest the presence of *N.* sp. *h.* Such characters as shallower pores, less angular shape and slightly coarser sculpture could then be used to separate doubtful examples and confirm the identification of *N.* sp. *h.*

*Distribution.*

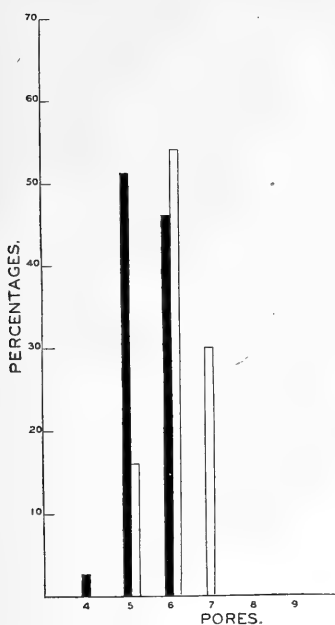
*Lignites:* Moorlands.

*Mudstones:* Balcombe Bay.

TABLE 8.

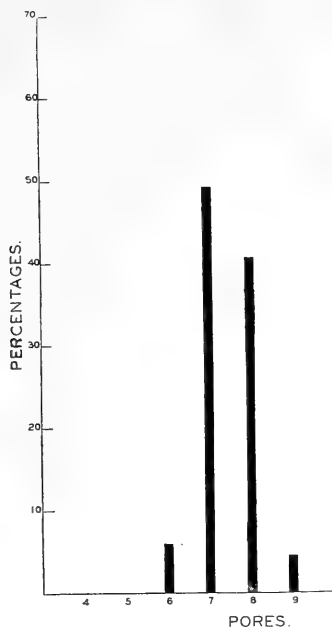
Locality.	Size-Range.	Average Size.	Pore-Range.	Pore-Maximum.
Balcombe Bay .. ..	29.0-48.0 $\mu$	36 $\mu$	6-9	49% 7
Moorlands .. ..	26.6-42.5 $\mu$	34 $\mu$	6-9	58% 7





Text-fig. 8.

Text-fig. 8.—Pore-frequencies in *N. sp. g.* ■ Vegetable Creek; □ Beenak.



Text-fig. 9.

Text-fig. 9.—Pore-frequencies in *N. sp. h.* from Balcombe Bay.

*Nothofagus sp. i.* (Plate ii, figs. 36-38. Text-fig. 10).

*General remarks.*—Type locality Moorlands; so far not observed in preparations from other deposits.

*Grain.*—Bi-convex, slightly angular in polar view. Size-range 26.6–47.5 $\mu$ , average 36 $\mu$ . Pores 6–9, majority 7, sunken about 2.5 $\mu$ .

*Exine.*—Firm, about 2 $\mu$ , forming short rims of the same thickness around the pores. Sculpture medium, clear; papillae pointed, but so extremely short that the exine when viewed in optical section appears smooth.

*Affinity.*—Although at present *N. sp. i.* appears to be an uncommon type, its characteristics seem sufficiently defined to warrant specific distinction. Its most striking feature is the shallow position of the pores, a feature it shares with members of the *fusca* group and *N. sp. d.* Approach to the former is made also through the clear but abbreviated papillae.

It is possible that *N. sp. i.* represents a stage in the evolution of the *N. fusca* pollen-type; the absence of especially thickened pore-rims and the pointed nature of the short papillae being distinguishing and perhaps primitive characters.

*Distribution.*

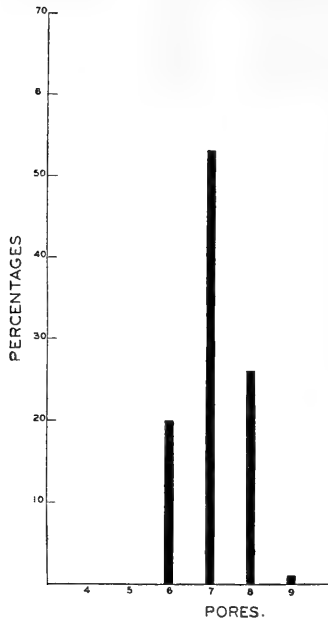
*Lignite:* Moorlands.

*Nothofagus sp. j.* (Plate ii, figs. 39-45. Text-fig. 11).

*General remarks.*—One of the more uncommon varieties, characterized by a heavy echinate sculpture.

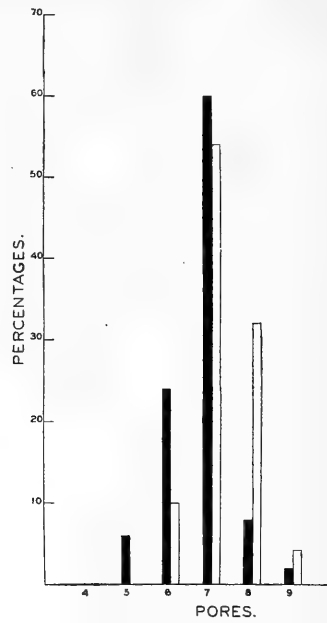
*Grain.*—Flattened, in polar view strongly angular. Size-range 26.6–40.0 $\mu$ , average about 34 $\mu$ . Pores 5–9, majority 7, the relative frequencies of 6 and 8 pores varying in preparations from different deposits (Text-fig. 11); sunken to a depth of from 4–5 $\mu$ .

*Exine.*—Firm, approximately 1.50–1.75 $\mu$ , forming decided but unthickened rims to the pore slits. Sculpture strongly developed; papillae crowded, coarse, always larger at the poles, basal diameter up to 2.5 $\mu$ , length from 1.0–2.5 $\mu$ , usually terminating in a sharp point but sometimes appearing as blunt, irregular tubercles.



Text-fig. 10.

Text-fig. 10.—Pore-frequencies in *N. sp. i.* from Moorlands.



Text-fig. 11.

Text-fig. 11.—Pore-frequencies in *N. sp. j.* □ Altona; ■ Budgeree.

*Affinity.*—*N. sp. j.* is clearly separated from the pollens described above by the characteristic prominence of the sculpture. In general form, size, and pore-number it comes nearest to *N. sp. h.* Since it has been observed in sufficient numbers for statistical purposes from only two deposits, however, any further discussion of affinity to other species is postponed until more information concerning these extinct types as a whole is available.

*Distribution.*

*Lignites:* Moorlands, Altona, Beenak, Budgeree.

*Mudstones:* Balcombe Bay.

KEY TO THE SPECIES.

- A. Grain opening by fissures .. .. . *N. sp. a.*
- Grain with functional pores .. .. . B
- B. Pores not deeply sunken .. .. . C
- Pores deeply sunken .. .. . F
- C. Exine of even thickness .. .. . *N. sp. i.*
- Exine thicker around pores .. .. . D
- D. Grain large, average size exceeding 35 $\mu$  .. .. . *N. sp. c.*
- Grain small, average size less than 35 $\mu$  .. .. . E
- E. Papillae short .. .. . *N. sp. b.*
- Papillae prominent, echinate .. .. . *N. sp. d.*
- F. Exine delicate, average size 40 $\mu$  or more .. .. . *N. sp. g.*
- Exine firm, average size less than 40 $\mu$  .. .. . G
- G. Pore-maximum 6 .. .. . H
- Pore-maximum 7 .. .. . I
- H. Papillae close, exine approximately 1 $\mu$  .. .. . *N. sp. e.*
- Papillae scattered, exine approximately 2 $\mu$  .. .. . *N. sp. f.*
- I. Sculpture fine .. .. . *N. sp. h.*
- Sculpture coarse .. .. . *N. sp. j.*

## SUMMARY.

The present analytical investigation supports the conclusion, drawn by previous workers from macroscopical studies of leaf-remains, that southern beeches were specifically more numerous in Australia during the Tertiary Period than at the present time. Previously von Ettingshausen (1888) distinguished six species of *Nothofagus* from beds in New South Wales and one from Tasmania, while Deane (1902) added two Victorian species to the number.

This study shows that an even greater variety of forms existed. Ten distinct pollen-types are figured and described, and there is some evidence that later more may be distinguished.

The distribution of fossil *Nothofagus* spp. as recorded by other investigators (Chapman, 1937; Deane, 1902; von Ettingshausen, 1888) is confirmed. By means of their pollens, they have been traced from South Australia to northern New South Wales, but no decision has been reached regarding the northward extension of the genus into Queensland during Oligocene-Miocene times. *N. Moorei* has a restricted distribution there to-day but lignite from Water Park Creek near Rockhampton has failed as yet to yield beech pollens.

An early date, possibly pre-Middle-Miocene, has been established for the definition of the two pollen-groups characteristic of *Nothofagus*. *N. sp. a.* is an undoubted example of the *Menziesii* type whereas *N. spp. b.* and *c.* are as clearly members of the *fusca* group.

In addition to, and associated in deposits with these, are types that cannot be so placed. They are pollens of presumably more primitive extinct species some of which may even represent stages in the evolution of more modern forms.

Statistics obtained from pore-counts (Text-figs. 2-11) support the suggestions of other workers (Cranwell, 1939, p. 191; von Post, 1929) that pore-frequency when considered in conjunction with other diagnostic features has a definite value in the separation of *Nothofagus* pollens. Of the pollens discussed here three are mainly 5- and 6-pored, while in the remaining seven species the prevailing pore-number is 7. This predominance of 7-pored pollens in the fossil as well as in the living species brings the Australian forms into line with New Zealand species where also 7-pored pollens are in the majority. The South American species of the *fusca* group (Cranwell, l.c., p. 189), on the contrary, have low pore-numbers in which 5 and 6 are by far the most numerous.

Finally it has been demonstrated that the sculpture of the exine is more pronounced in the fossil pollens than it is in those of the living species. The papillae in the former are usually clearly defined and more or less strongly echinate.

## ACKNOWLEDGEMENTS.

It is with pleasure that I express my indebtedness to the following geologists who have generously supplied me with information and much of the material necessary for this work: Sir Douglas Mawson and Dr. Keith Ward in South Australia; Mr. W. Baragwanath, Professor E. S. Hills, Dr. F. A. Singleton, Dr. A. E. Edwards and Mr. G. Baker in Victoria; Dr. Ida A. Brown and Dr. J. A. Dulhunty in New South Wales; Mr. A. W. Beaseley in Queensland; and Dr. C. Teichert in Western Australia.

Samples of lignite from specified levels in the Yallourn open cut and lignite and ligneous clays from bores at Maryvale have been provided by the courtesy of Mr. J. N. Bridge and Mr. R. J. McKay of the State Electricity Commission, whose helpful interest I appreciate.

For pollens of living species I owe gratitude to Mr. A. W. Jessep and the staff of the National Herbarium, Melbourne; Mr. E. J. Sonenberg, Melbourne University; Mr. R. H. Anderson, National Herbarium, Sydney; and Mr. W. F. Harris and Mr. George Simpson of New Zealand.

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## EXPLANATION OF PLATES I-II.

All the figures are from untouched negatives. All represent polar views of pollens of *Nothofagus* spp. at a magnification of 625 diameters.

## Plate i.

- Fig. 1.—*Nothofagus Menziesii*. A partially ruptured grain showing 7 fissure-points.
- Fig. 2.—*N. Cunninghami*. An acetolysed grain showing one fissure and positions of 6 fissure-points. Otway Forest, Victoria.
- Fig. 3.—*N. Cunninghami*. Grain with 2 widely open fissures. Otway Forest, Victoria.
- Fig. 4.—*N. Moorei*. Grain showing 8 fissures. Near headwaters of the Manning River, New South Wales.
- Fig. 5.—*N. sp. a*. Grain showing 8 fissure-points. Vegetable Creek, New South Wales.
- Fig. 6.—*N. sp. a*. A partially ruptured grain with 7 fissure-points. Vegetable Creek, New South Wales.
- Fig. 7.—*N. sp. a*. A large completely ruptured grain showing 8 deep fissures. Bore 155, 552 feet, Maryvale, Victoria.
- Fig. 8.—*N. sp. b*. A 7-pored grain. Bore 155, 552 feet, Maryvale, Victoria.
- Fig. 9.—*N. sp. b*. A 7-pored grain. Anglesea, Victoria.
- Fig. 10.—*N. sp. b*. A 6-pored grain. Moorlands, South Australia.
- Figs. 11, 12.—*N. sp. b*. 6-pored pollens showing coarse sculpture. Vegetable Creek, New South Wales.
- Fig. 13.—*N. sp. b*. Grain focussed to show sculpture. Moorlands, South Australia.
- Figs. 14, 15.—*N. Gunnii*. Acetolysed grains. Cradle Mountain, Tasmania.
- Fig. 16.—*N. fusca*. Acetolysed grain focussed for sculpture. Eglinton Valley, New Zealand.
- Fig. 17.—*N. sp. c*. Large 7-pored grain. Bore 155, 552 feet, Maryvale, Victoria.
- Fig. 18.—*N. sp. c*. 6-pored grain, Lal Lal, Victoria.
- Fig. 19.—*N. sp. d*. 6-pored grain. Yallourn, S.E.C., sample 6, 150 feet from top of coal.
- Fig. 20.—*N. sp. d*. 6-pored grain. Budgeree, Victoria.
- Fig. 21.—*N. sp. d*. 7-pored grain. Yallourn, S.E.C., sample 6.

## Plate ii.

- Fig. 22.—*N. sp. e*. 6-pored grain with closed pore-slits. Bore 155, 552 feet, Maryvale, Victoria.
- Figs. 23, 24.—*N. sp. e*. 6- and 7-pored grains with partially open pore-slits. Kiandra, New South Wales.
- Fig. 25.—*N. sp. e*. 5-pored grain with widely open pore-slits. Yallourn, S.E.C. sample 4, 92 feet below top of coal.
- Figs. 26, 27.—*N. sp. f*. 5- and 6-pored grains. Boolara, Victoria.
- Fig. 28.—*N. sp. f*. 6-pored grain focussed for sculpture. Boolara, Victoria.
- Fig. 29.—*N. sp. f*. 6-pored grain. Moorlands, South Australia.

\* Original paper not available.

- Fig. 30.—*N. sp. g.* 5-pored grain. Vegetable Creek, New South Wales.  
Fig. 31.—*N. sp. g.* 6-pored grain. Moorlands, South Australia.  
Fig. 32.—*N. sp. g.* 7-pored grain. Beenak, Victoria.  
Figs. 33-35.—*N. sp. h.* 7-, 8-, 9-pored grains. Balcombe Bay, Victoria.  
Figs. 36-38.—*N. sp. i.* 7- and 8-pored grains. Moorlands, South Australia.  
Fig. 39.—*N. sp. j.* 5-pored grain. Budgereee, Victoria.  
Fig. 40.—*N. sp. j.* Grain with partially open pore-slits. Altona, Victoria.  
Fig. 41.—*N. sp. j.* 6-pored grain with open pore-slits. Altona, Victoria.  
Fig. 42.—*N. sp. j.* 7-pored grain. Balcombe Bay, Victoria.  
Fig. 43.—*N. sp. j.* 7-pored grain. Budgereee, Victoria.  
Fig. 44.—*N. sp. j.* 7-pored grain showing papillae in relief. Beenak, Victoria.  
Fig. 45.—*N. sp. j.* 8-pored grain. Moorlands, South Australia.
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## MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. XII.

CYRTIDAE, DOLICHOPODIDAE AND PHORIDAE.

By G. H. HARDY, Queensland University, Brisbane.

(Three Text-figures.)

[Read 27th March, 1946.]

## THE VENATION OF DIPTERA.

Lundbeck (1907, p. 8) states that "the important observations of Adolph concerning the convexity and concavity of veins must absolutely be taken into consideration" when homologizing the venation in the various families of Diptera. Early authors also discussed the matter in papers of which only that of Brauer (1882) is before me. As Alexander has shown that two or more veins may be compounded and developed to look like a simple vein, notwithstanding its complex nature, those observations of early authors may be viewed in a new light and the explanation found that will account for many anomalies in wing venation.

Difficulty at times will be met in making out the convexity and concavity of veins where the wings have been flattened, especially at the apical margin of the wing; however, on newly emerged flies the contrasting convexity and concavity is strongly marked, as it is also in most specimens of the more primitive flies in the lower Brachycera. In the Nemestrinidae this feature may be entirely obscured in the median branches, making it advisable to leave without comment that family for the time being.

Judgment is made as to whether the veins are on the crest (convex) or in the furrow (concave) on the upper surface of the undulating wing membrane, but a vein may take the normal course along the crest and proceed into a furrow, thus taking in part the course of a cross-vein. A convex and a concave vein may coalesce in part, and the nature of the coalescing part will be determined as convex or concave by the vein which dominates, this usually being the convex vein. It is not clear yet how such complex veins are to be notated in a satisfactory manner, but it is considered necessary to take some action in these notes in order to clarify the position.

Tillyard (1926) has given the theoretical condition for each branch of the varied fields and Brauer (1882) has given the actual nature of the branches as found by him; these are tabulated below. The most recent discussion on the subject seems to be that by Lundbeck (1907), who includes a figure illustrating the character of all veins.

*Table of Venation.*

Name of Branch.	Theoretical Character (Tillyard).	Actual Character (Brauer).	Number (Brauer).
Costa .. .. .	not stated	convex	—
Subcosta .. .. .	concave	concave	H.
Radial 1st .. .. .	convex	convex	1
" 2nd .. .. .	concave	(absent)	—
" 3rd .. .. .	"	concave	2
" 4th .. .. .	"	convex	3
" 5th .. .. .	"	"	3
Median 1st .. .. .	"	"	3
" 2nd .. .. .	"	"	3
" 3rd .. .. .	"	concave	4
" 4th .. .. .	"	convex	5
Cubital 1st .. .. .	convex	"	5
" 2nd .. .. .	concave	—	—
Anal 1st .. .. .	convex	concave	6
" 2nd .. .. .	concave or convex	convex	7

Brauer has numbered his scheme of venation on a system that makes clusters of branches alternating convex (odd numbers) and concave (even numbers) in a manner as he found them to occur. As the anal area has both a convex and a concave vein, Lundbeck suggested that these should be given different names each applicable to the one which happens to be left in the wing of the Brachycera as both forms are present in the group and are standing under the one name. He made no reference to the anal vein which is partly of a convex and partly of a concave nature, but this may be compounded of the two, and there may be some evidence to support the contention.\*

#### Family CYRTIDAE.

It is uncertain if the Cyртоidea have the first median vein coalescing with  $R_5$ , but if so then the second radial-median cross-vein becomes  $M_1$  and, by subsequent numbering, the vein called  $M_3$  becomes an intermedian cross-vein between  $M_3$  and  $M_1$ , as already indicated in an alternative notation given for the venation in the Nemestrinidae.

The notation used here for the genus *Panops* is that usually used in the family and to it has been added, by mathematical signs, the nature of the vein, whether it be convex (+) or concave (-). This venation is the most complete known in the family, and the key to the Australian genera is largely based upon it.

#### Key to Genera of the Cyrtidae.

1. With a complete set of wing veins, or practically so. With the antennae long and situated high on the head ..... 2  
 With a much reduced venation. With the antennae short and situated very low on the head ..... 3
2. With the eyes meeting above the antennae which are thus separated from the ocelli. With appendix present ..... *Leucospina* Westw.  
 With the antennae adjacent to the ocelli; the eyes, being separated, leave a short square-shaped frons between them. With appendix sometimes absent ..... *Panops* Lamarck
3. With only one median vein reaching the wing border between the radial and cubital fields. With the median section lying between the two radial-median cross-veins eliminated .. 4  
 With few veins retained; none of the median branches reach the wing margin ..... *Oncodes* Latreille
4. With the anterior margin of the wings strongly curved forwards at the apex of the costa ..... *Pterodontia* Gray  
 With the anterior margin of the wings normal in shape ..... *Nothra* Westwood

#### Genus PANOPS Lamarck 1804.

Synonym.—*Epicerina* Macquart 1849; for reference to this and all other genera see Hardy, *Proc. Roy. Soc. Tasm.*, 1921: 75–80.

This synonymy has been suggested before, but now it seems certain. The type of *Epicerina* is said to be from Tasmania but it belongs to those flies mostly caught in the Sydney area and described by Macquart in his fourth supplement as being all from Tasmania. Three species now stand under this genus.

*P. baudini* Lamarck, ♂ and ♀, genotype, has no appendix and the abdomen is conical.

*P. nigricornis* Macquart, ♂ and ♀, has the appendix, and the abdomen is conical. This has not yet been detected in Australian collections and it may be doubted if the proboscis is short, as stated by Macquart.

*P. flavipes* Latreille, ♂ only known, has the appendix and the longer abdomen which is constricted at segmentations giving the "corrugated" shape. Tillyard (1926, Pl. 23, fig. 12) has illustrated it under the name of *baudini*.

#### PANOPS FLAVIPES Latr. Fig. 1.

The presence of two adjacent ridges of thickened membrane is an aberrant character that occurs between  $R_{1+2}$  and  $R_3$  of one wing only on one specimen before me, and it evidently marks the course of the obsolete branch  $R_3$ . The length of the appendix is variable and the convexity and concavity of the veins stand with remarkable clarity.

\* I have not yet met with evidence, but Williston (1908) has illustrated the wing of *Acanthomera* with Brauer's veins 6 and 7 coalescing at their base (i.e., "stalked") and it is only necessary to eliminate the free part of vein 7 to bring about this case (noted on *Panops*) of a basally convex and apically concave anal vein, with the division between the convex and concave part quite abrupt.



The second radial-medium cross-vein,  $M_2$  and  $i-m$  are, however, quite neutral, but  $M_3$  carries with it a definite furrow which strongly suggests that it cannot be a cross-vein. The fourth radial branch and the first median are concave and the basally-convex and apically-concave anal vein all differ from the normal. Other veins are normal. An ambient vein is present, reaching to the apex of the cubital vein. Hair occurs on the membrane between the apices of Sc and  $R_{1+2}$ .

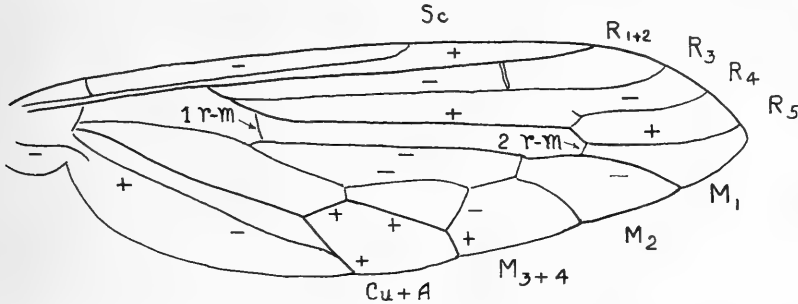


Fig. 1.—The venation of *Panops flavipes* Latr., illustrating those veins which are convex (+) and concave (-). The veins 2  $i-r$ ,  $M_2$  and  $i-m$  are neutral, being in a small flattened area of the wing membrane.

The proboscis reaches to the second abdominal segment and the abdomen has six observable segments complete; the seventh sternite and the hypopygium are also distinctly visible.

*Hab.*—New South Wales and southern Queensland. Three specimens examined. I have met with this species twice only, once near Sydney and once at the large swamp at Sunnybank, Qd., both occasions being in October. A specimen in the Queensland Department of Agriculture is labelled “Stanthorpe, 2.11.1927” and bears a supplementary label with “S. M. Watson”. It is an unusually large specimen and the above notes are taken from this, as also the sketch of the venation.

Superfamily ASILOIDEA.

The manner in which the Dolichopodidae have derived their peculiar venation has given a clue to the formation of a phylogenetical treatment of families centred around the Empididae. The Lonchopteridae may have derived their venation from the Empid type as there is no evidence to suggest otherwise. In this case  $R_5$  and  $M_1$  do not coalesce as in the Dolichopodidae and presumably in the Platypezidae, too. It seems that *Sciadocera*, originally described as an Empid, has its veins reduced from the Dolichopod type and so belongs to that stem.

Key to the Empid-Dolichopod Complex.

1. The first median branch ( $M_1$ ) never coalescing with the fifth radial branch ( $R_5$ ). The subcosta reaching the costa independently, but sometimes it is reduced in length . . . . . 2  
The first median vein coalescing apically with the fifth radial vein, with the course of  $R_5$  broken between the point of meeting and the interradial cross-vein ( $i-r$ ) . . . . . 3
2. The arista two-segmented at most. The venation varies and only a few veins may be retained, but usually the median cell is present . . . . . EMPIDIDAE  
The arista three-segmented. The venation is much reduced and the median cell is absent . . . . . LONCHOPTERIDAE
3. Arista two-segmented, but sometimes it arises from a tubercle which looks like another segment. Venation variable but the subcosta, when complete, coalesces apically with the first radial branch . . . . . DOLICHOPODIDAE  
The arista three-segmented . . . . . 4
4. The subcosta coalesces apically with the first radial branch . . . . . genus *Sciadocera* White  
The subcosta normally reaches the costa but sometimes it is incomplete . . . . . PLATYPEZIDAE

The genus *Sciadocera* is best appended to the Dolichopodidae as it agrees there in head, tarsi and leg adornment.

Family DOLICHOPODIDAE. Fig. 2.

The radial field has been reduced to three apparent branches and the way in which this has been accomplished is given in a series of figures that shows the stages developed

from the Empid type to that median character found on *Dolichopus zickzack* Wied. In this species, in the genus *Vaalimyia* Curran, and in various South American species of Chrysosomatinae, there is an appendix attached to the second bend of the so-called first median branch. This appendix marks where  $M_1$  has coalesced with  $R_5$  which itself is interrupted between the appendix and the interradial cross-vein. The radial sector is reduced to two apparent branches,  $R_3$  and the basal part of  $R_5$  in continuity with  $i-r$  and the apical part of  $R_1$  which reaches the wing margin. The first median branch is basally coalescing with  $M_2$  from which arises the free part of  $M_1$ , whilst further on in its course  $M_1$  coalesces with the apical part of  $R_5$ . This reduction becomes more pronounced by the

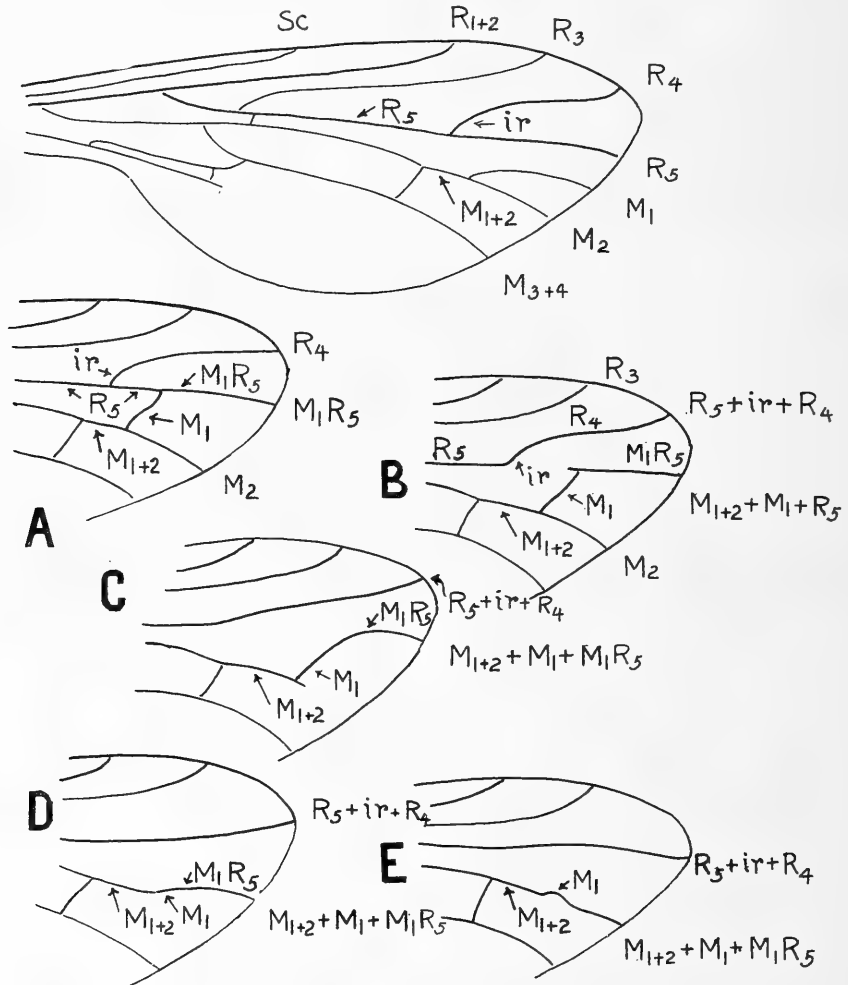


Fig. 2.—The venation of an Empid having the full complement of veins in the radial and median fields, but with  $M_1$  and  $M_2$  coalescing at their bases. From this can be traced the condition which occurs in the Dolichopodidae. In A, the branch  $M_1$  coalesces with  $R_5$  at its apex, and in B, the vein  $R_5$  is interrupted between this point of coalescence and the interradial cross-vein, leaving a small appendix to mark the free part of  $R_5$  at its union with  $M_1$ . Further stages in this development are seen in C, where the branch  $M_2$  begins to disappear, whilst the compounded vein  $R_5 + i-r + R_4$  tends to straighten out. In D, this reaches a stage where the compounded vein  $M_{1+2} + M_1 + R_5 M_1$  also tends to straighten, reaching the condition in E where a kink is left (and seldom absent) to mark the position of the free part of  $M_1$ . In extant forms the radial field is left with three more or less straightened veins, and the median field retains types illustrated in B to E, that of A being the hypothetical stage that accounts for the origin seen in the Empid type of venation.

elimination of the free part of  $M_2$  and the appendix. The zig-zagging veins remaining tend to straighten out in the normal way, and in so doing, the last sign of this amalgamation is noted in the kink that represents the free part of  $M_1$ . This kink is rarely absent in the venation of advanced genera of the family. Thus it is seen that here the vein  $M_1$  of taxonomists is the complex  $M_{1+2} + M_1 + M_1R_5$ . The vein  $R_{4+5}$  becomes the complex  $R_5 + i-r + R_4$ . Owing to the normal venation of the Platypezidae being like the more primitive types in the Dolichopodidae, it seems certain that this family derived its venation in a similar way. The same applies to *Sciadocera* as the venation retained lies in the same form as those veins here discussed.

DOLICHOPUS ZICKZACK Wiedemann.

It is not known if this species, which ranges from India to Queensland, is a complex. *Lichwardtia formosa* Enderlein (1912) was placed as a synonym by Becker (1922); Curran (1926) has since erected the genus *Vaalimyyia* from Africa and to this the present species seems related. Lichwardt described his species under Chrysosomatinae but its position there has not been accepted.

SCIADOCERA RUFOMACULATA White. Fig. 3.

White 1917, *Proc. Roy. Soc. Tasm.*, 1916: 218. Tonnoir 1926, *Rec. Cant. Mus. N.Z.*, 3: 31-8, Pl. 4 (as *maculata* in error).

This unique fly was described from Tasmania under the Empididae by White, but Tonnoir regarded this position as unsatisfactory and so relegated it to the Phoridae with which he saw some resemblance in venation and terminalia. The venation, however, does not conform sufficiently, and the terminal part as drawn by Tonnoir is unsatisfactory, as he missed the aedeagus at least. Tonnoir concluded his discussion with: "I believe, therefore, that there is not the least affinity between *Sciadocera* and the Empididae; if some were looked for with a family of the Brachycera it would be rather with the Dolichopodidae, on account of the shape of the head, the posterior row of bristles, the structure of the antennae, and Sc fused distally with  $R_1$ ." He used the term Brachycera in a restricted sense.

It now becomes possible to show that the venation is nearer to the Dolichopod type than that of the Phoridae and the drawing here given is that of Tonnoir's figure with the free part of  $M_1$  restored by a broken line, the upper median main vein similarly completed and the intermedian cross-vein removed to a position more apically distant than actually found in the fly. At present it is not clear how this could possibly lead to the venation in a Phorid fly.

Following the sixth abdominal segment there is a small seventh tergite and beyond this an asymmetrical eighth tergite to which the hypopygium is attached. The hypopygium consists of the ninth segment reduced to a pair of side-plates dorsally placed,

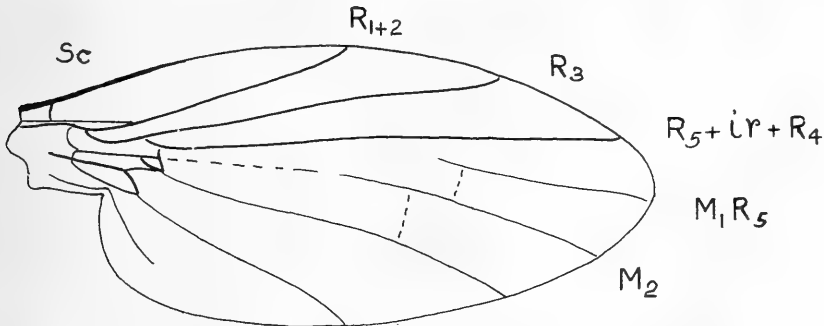


Fig. 3.—The venation of *Sciadocera* (after Tonnoir) added to which are broken lines representing veins needed to complete the figure to make its Dolichopod origin understandable. The added upper vertical vein is  $M_1$  which coalesces with  $R_5$ , and the added horizontal vein borders the median cell above. The added lower vertical line marks the position of the apical border of the median cell, the vein normally there having retreated to a position in alignment with the radial-median cross-vein.

and below them the presumed anal papilla (Phorid in shape and position), but no aedeagus and no claspers are shown. There is a ventrally-placed single sclerite, that is slightly asymmetrical and indented at the apex, whereas in the Phoridae there is a pair of latero-ventrally placed plates. If the hypopygium drawn by Tonnoir be an inverted one, then the anal papilla would become the aedeagus and the pair of dorsally-placed plates is the vestigial basi-styles of taxonomists, and the rest of the hypopygium as drawn becomes understandable. There is no evidence, however, that this is the true rendering, but probably the drawing is incomplete, parts being broken down, perhaps, by the caustic treatment which Tonnoir used in his mounting of terminal parts.\* Tonnoir states of the hypopygium that it is "not widely different to that of *Apiochaeta*". I have examined this Phorid and found a wide divergence from the drawings, but the anal papilla was reasonably like that of *Sciadocera*; Tonnoir, however, included the eighth segment with the hypopygium which added to the resemblance.

#### Family PHORIDAE.

The relationship of this family has been under constant dispute, but on larval and pupal characters it is generally included under the Cyclorrhapha. The terminal parts, however, are definitely Orthorrhaphous in type, and erect, as shown by the retention of the anal papilla lying above the aedeagus, and both these parts have the orifice directed rearwards. The venational characters are such as to suggest that either the radial and median fields coalesced, or the upper main branch of the median vein was eliminated in the part between two radial-median cross-veins, leaving the median branches joined to the radial field by incorporating these cross-veins in their development to form simple convex veins, the fifth radial being also incorporated perhaps with  $M_1$ . The radial field has the appearance of being three-branched but whether it passed through a process similar to that in the Dolichopodidae is problematical.

It would appear that the Phoridae were evolved from some pre-Syrphoidean type, and that they have developed too far to be classed with the Orthorrhapha and not far enough to have the circumverted hypopygium of the Syrphoidea. The aedeagus is unusual in form and incorporates an armature of a type unknown in either the Asiloidea or the Syrphoidea. The venation could have been derived from that of either the Tabanoidea or the Asiloidea. The similarity to the latter might be caused by convergence, but if the Cyclorrhapha be derived from the Dolichopod type, or from the Cyrtid type, as Crampton is inclined to think, is not yet clear. It may prove necessary to erect another superfamily for its reception, if the alliance of the Phoridae with Cyclorrhapha is to be maintained. This would render necessary another couplet in the key to superfamilies (Hardy, these PROCEEDINGS, 69: 80) and a slight alteration as follows:

- |  |              |   |
|--|--------------|---|
| A. Coxopodites (which include the primitive claspers) are present. Male terminalia rectilinear or else curvilinear with the eighth and ninth tergites adjacent to each other .....   | ORTHORRHAPHA | 2 |
| .....  | CYCLORRHAPHA | 1 |
| Coxopodites vestigial or absent .....  |              |   |
| 1. Male terminalia are rectilinear and the coxopodites vestigial, no claspers being formed .....   | PHOROIDEA    | 7 |
| .....  |              |   |
| Male terminalia either curvilinear combined with an inverted hypopygium so that the eighth tergite and ninth sternite are adjacent to each other, or else completely circumverted. The aedeagus is always directed anteriorly and lies within a phallic pouch, normally within the sixth abdominal segment ..... |              | 7 |

In the list of superfamilies (l.c., p. 79) it is necessary to insert under section Cyclorrhapha, the following:

Subsection .....	Hypocera
Superfamily .....	Phoroidea

The name *Hypocera* is in general use and was proposed by Schiner to incorporate the Phoridae only; it is, however, also a generic name and is not very suitable for the purpose, standing as it does, for the subsection and a genus under it. Coquillett (1891) proposed the superfamily name in which he also included the Lonchopteridae, but this addition has not been accepted. The superfamily Phoroidea now covers two families—

\* This defect is also noticeable in his rendering of the terminalia on *Pierretia australis* J. & T. (see these PROCEEDINGS, 68: 22).

the Phoridae and the closely-related Termitoxeniidae which is limited in distribution to Africa and India.

Tillyard placed *Braula* under Phoridae, but that genus has the typical circumverted aedeagus of the Muscoidea and therefore must be excluded.

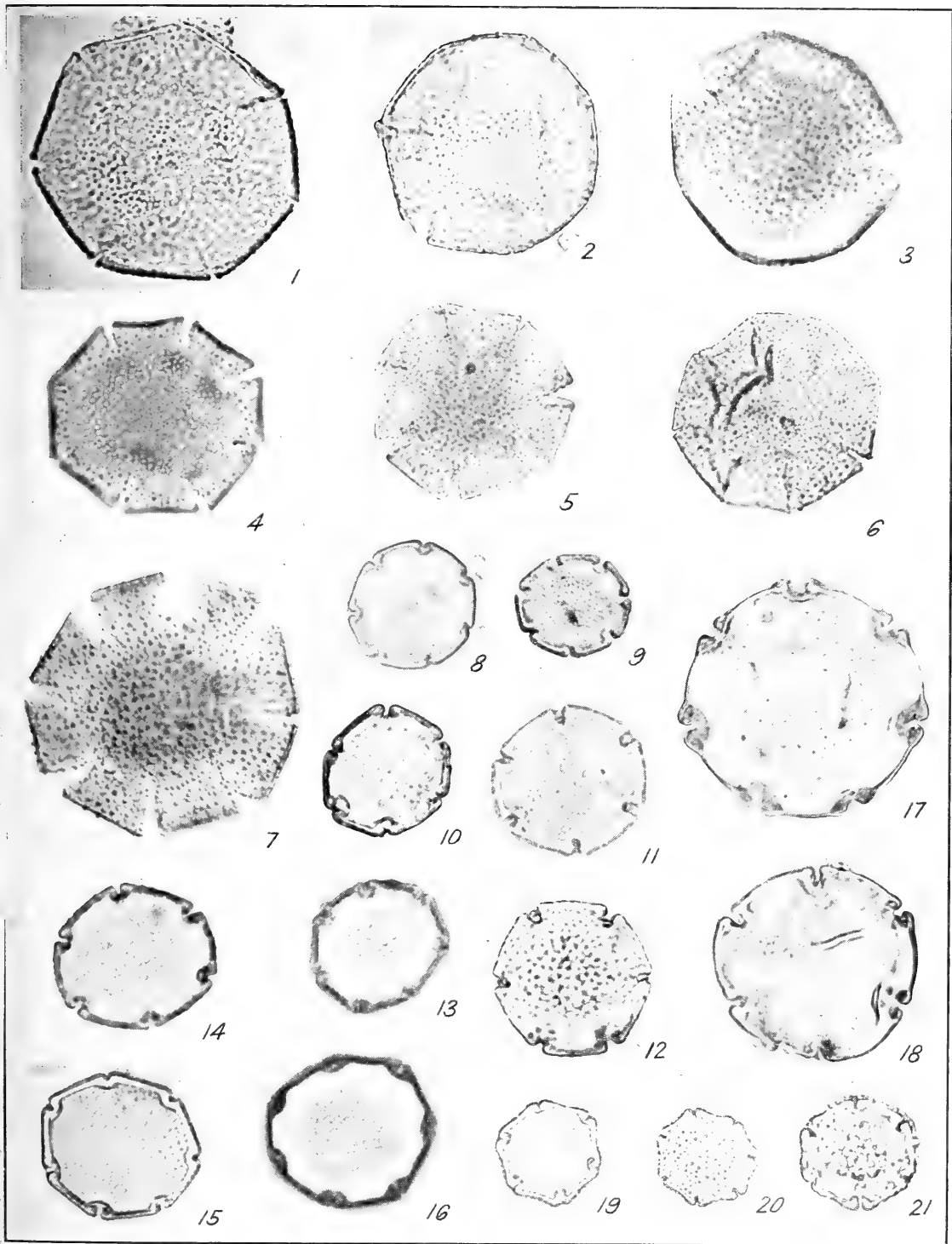
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\* References already given in parts x and xi of this series (these PROCEEDINGS, Vol. 69: 76-86 and Vol. 70: 135-146) are not repeated here.

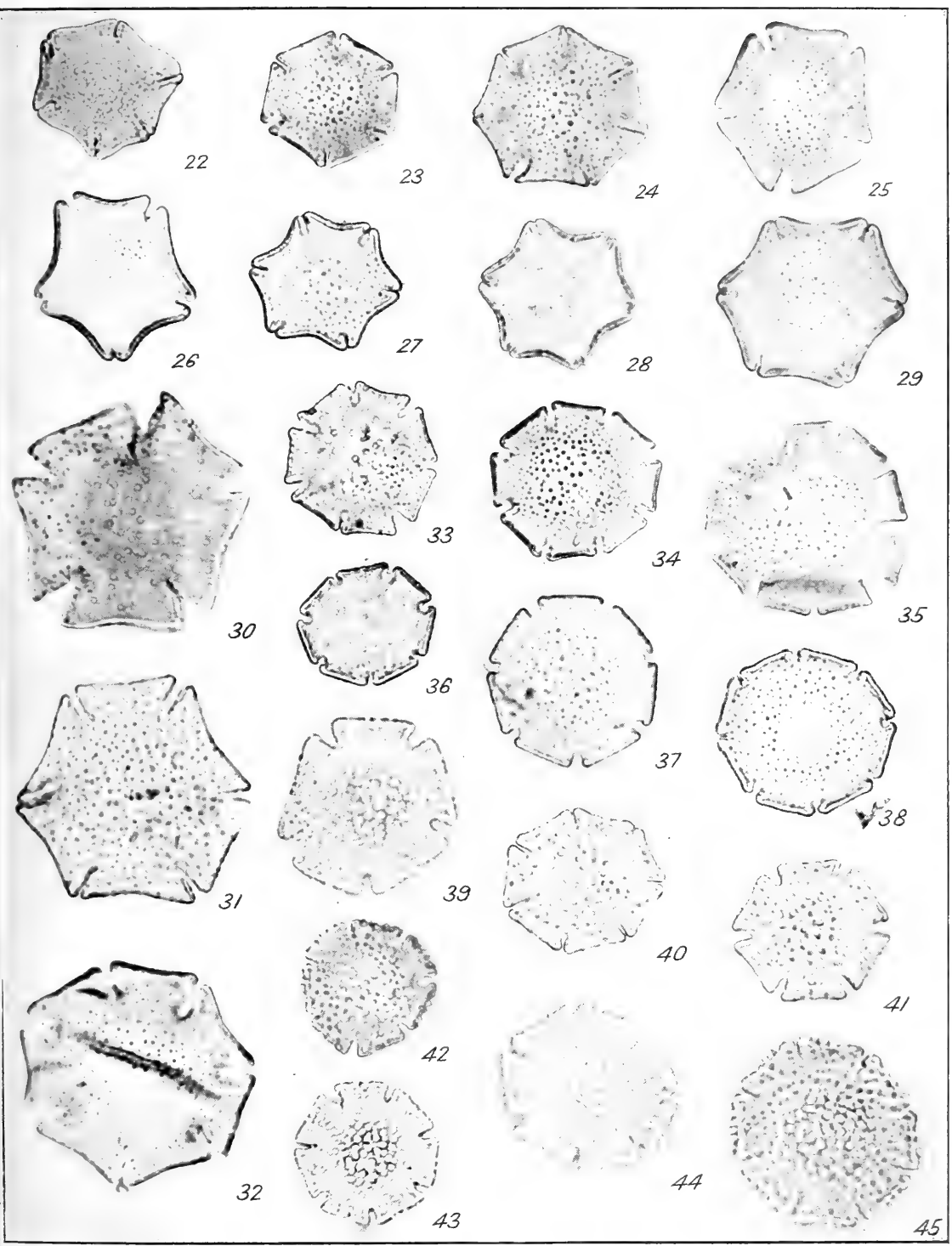




Pollens of *Nothofagus* from Tertiary Deposits in Australia.







Pollens of *Nothofagus* from Tertiary Deposits in Australia.



## THE EVOLUTION OF THE MAXILLO-PALATE.

By H. LEIGHTON KESTEVEN, M.D., D.Sc.,

(Forty-three Text-figures.)

[Read 26th June, 1946.]

### INTRODUCTION.

The term maxillo-palate has been introduced here to include as a single structural unit all the bones which contribute to the formation of the upper jaw, palate, false palate, and the bony roof of the mouth where that extends beyond the palatal bones. None of the terms in general use includes all these bones. The one suggested has the merit of relative brevity, of freedom from prior use and acceptance in any more restricted sense, and of freedom from ambiguity.

It is believed that we can hope to understand the evolution of the bones in any part of the maxillo-palate only if and when the *mechanics*, as well as the morphology, embryology and phylogeny of the structure as a whole and in part, are studied.

It is believed that if homologies are to be established in the presence of changes in form, mode of development, and/or function of bones, and are to be properly understood and interpreted, some *reason* for the change should be discoverable, in essentially the same way as a mechanical explanation is usually available for phylogenetic changes in direction, form and function of muscle fibres.

Whilst the basic concept of homology is homogeny (community of phylogenetic origin), it may be stated generally that those homologies which have been, and can be, accepted unreservedly are, for the most part, those in which the congruence of the mechanical factors and the morphological or embryological changes are self-evident or demonstrable.

As an example in illustration: In a quite general sense there has been a unanimity of opinion that bones which develop as cartilage bones are unlikely to be homologous with bones which develop as membrane bones. Yet the complete homology of the supra-occipital bone throughout the Vertebrata has never been questioned, although in some forms it develops as a membrane bone, in others as a cartilage bone. The evidence against the homology of the bones presented by the changed embryological history is far outweighed by the evidence in favour of the homology presented by the constancy of the topographical relations to other structures. But underlying this conclusion, there has always been, whether realized or not, the complete *reasonableness* of the conclusion. In view of the obvious stasis of all the mechanical factors, no other interpretation could be put upon the presence of the bone than to assume that it was the same bone with a changed ontogeny.

There is one outstanding example of a general agreement to regard as homologous bones which are completely dissimilar, and this in the absence of any reason in explanation of the change. The reference here is to Gaupp's theory of the inclusion of a cavum epiptericum in the therian cranial cavity, and the homology of the processus ascendens quadrati with the alisphenoid bone in the therian skull.

This is a particularly interesting example, because, since the theory was first propounded, a great deal of evidence directly opposed to the theory has come to light, and all this evidence has been interpreted on the assumption that the theory was completely proven.

Edgeworth's comment: "The theory that the ala temporalis, an upgrowth of a lateral process of the chondrocranium, is homologous with an upgrowth of the palato-

quadrate, which is an entirely different structure, may be acceptable to some, but for me is a too difficult an exercise in belief" (1935, p. 69), probably fairly presents the mental attitude of every student who has attempted to discover any *reason* why the profound changes postulated should have come about, for none is discoverable.

In the attempt to visualize the evolution of the vertebrate palate which follows, the effect of mechanical factors, evident, probable, or possible, have been constantly kept in mind.

In short, an attempt has been made to explain *why*, as well as morphologically and/or embryologically *how*, the changes observed or postulated have come about.

After some hesitation, the series of short descriptions and the illustrations have been given as Part ii. Much of the information will be familiar to many readers. It has been given as a ready reference to refresh the memory of each reader in the facts he may not remember clearly.

#### THESIS.

It is thought that the various types of arrangement of the bones in the maxillo-palates of the vertebrate groups can be most reasonably explained on the following assumptions, all of which are supported by, and shed light upon, the facts observable:

1. The number of bones on the palato-quadrate arch was determined in an elasmobranchian ancestor.\*
2. This number of bones is present in all the early maxillo-palates.
3. The palato-quadrate arch became attached in front on each side of the ethmoid cartilage.
4. The premaxillae and maxillae, already present on the palato-pterygoid, became fused with dermal ossicles and acquired a new relation to the ethmoid cartilage. The persistence of the two bones thus formed, throughout the whole of the later changes, was largely conditioned by the unchanging nature of the function they were called upon to discharge.
5. The bony fish maxillo-palate was not further modified in the manner of its attachment to the skull. It remained slung behind by the hyomandibular cartilage or bone, and was articulated, not rigidly attached, in front, to permit of respiratory movements.
6. The maxillo-palate of the tetrapods became rigidly fixed both in front and behind, the hyomandibular suspension giving place to a rigid attachment by the quadrate. As a result, the whole maxillo-palate was drawn up flush with the base of the skull and the parasphenoid came to function as the posterior part of the bony roof of the mouth. The typical amphibian maxillo-palate was evolved in this manner.
7. The parasphenoid bone became fragmented in some forms and was replaced by two symmetrical bones developed from the stroma of the parent bone. The *reason* for this fragmentation is not apparent, but the morphological evidence appears fairly strong. This fragmentation of the parasphenoid resulted in the formation of the saurian pterygoid bones and the evolution of the saurian and ultimately the therian maxillo-palate.

#### PART I.

##### DISCUSSION.

##### *Introduction.*

This work was commenced as a study of the phylogeny of the bones in the therian palate, but it very early became apparent that sufficient evidence was not available for such a study. Almost at the outset it was found that it would be necessary to decide, in respect of every palate regarded as a possible precursor to another, whether the

\* The evidence in support of this is slight but exceedingly significant. The number of bones in question is present on the palato-quadrate of *Acipenser*. This leads to the belief that a careful study of the bones in the maxillo-palate of fossil Chondrostei may be expected to reveal, not only intermediate stages in the conversion of the free elasmobranchian suspension to the anteriorly attached suspension, but also that the same number of bones were present in the maxillo-palate.

arrangement of the bones and/or their degree of development was primitive, degenerate, or specialized. Clearly it is such only as are primitive, actually or relatively, that may be regarded as early, or earlier than others, and, therefore, as presenting a phylogenetic stage in the evolution of the vertebrate palate.

Unfortunately, every such decision would be merely an expression of opinion; there is really no factual evidence on which decisions may be based.

On the other hand, it is possible to arrive at satisfactory conclusions relative to the probable homology of the bones in the various palates without determining whether the palates being studied are primitive, degenerate, specialized, or advanced. Obviously, if primitive, the arrangement and degree of development of the bones may be deemed to present the early form. If degenerate, then the features seen must have degenerated from some other form, and its component bones must be homologous with those of the normal type from which it has degenerated. If specialized, its components will be homologous with those of the normal type from which its specialization has caused it to depart. If advanced, its components must be homologous with those of the form from which it has progressed.

The writer has brought to this work a familiarity with the evolution of the muscles of the head and neck, from fish to mammal. The observations made in the course of that study lead to two conclusions. Firstly, many muscles present in the lower forms were completely lost in the higher, and secondly there was no room for doubt that every one of the muscles in the higher forms had been evolved by modification of muscles already present in the lower. In other words, no evidence was found to support a belief that entirely new muscles have appeared in any form. There appeared to be ample evidence to support a belief that the division or fusion of myogenetic stromata present in more primitive forms had given rise to muscles present in more advanced types.

Throughout that investigation it appeared obvious that both skeletal and muscular structures were exceedingly plastic and were modified together to adapt the whole to changing modes of life which entailed altered mechanical conditions. The modifications of muscles were, in some instances, so profound that, whilst one was confident that a given muscle B was definitely derived from a more generalized form A, its form and function were so completely different that one hesitated to call the two homologous.

It is, therefore, as well to state what the writer intends to convey by the term "homologous". A rigid definition of the term would probably be the following:

If it be demonstrated that a given structure or organ in different species has been developed phylogenetically from a precursory structure or organ in an ancestor common to the species in question, then the structure or organ in question is homologous.

Since phylogeny cannot be observed, it is clear that homology can never be demonstrated. We are therefore constrained to adopt some less rigid "working" definition. The following presents the writer's concept of such, as applicable to the present study:

It is permissible to regard bones in skulls of different animals and fishes as homologous if it is reasonable to believe that they have been developed phylogenetically from the same bone in a common ancestor.

The evidence on which the belief should be based may be set out as follows:

- I. Its adult topography.
  - (a). Spatial relation to the bones and/or cartilages of the skull, including nasal and otic cavities.
  - (b). Spatial relation to the bones and/or cartilages of the visceral arches.
  - (c). Spatial relation to soft structures, especially nerves, blood-vessels and muscles.
- II. The relation of the bone to the dermis.
- III. The relation of the bone to the mucosa of the mouth.
- IV. The embryology of the bone, with especial reference to its genetic relation to other structures.
- V. The whole of these criteria to be studied under the light thrown upon the changes, evident or thought to have taken place, by the mechanical factors known or thought to have been acting.

When all these criteria do not point to the same conclusion, it becomes necessary to weigh one group against another before coming to a decision.

In the discussions the numerical designations used in Part ii will be used whenever such use will avoid loading the text with wordy conflict of nomenclature, but, for the most part, the bones will be referred to by the names most generally applied in the past, using inverted commas if the designation is not that adopted in the table of nomenclature set out below.

TABLE OF NOMENCLATURE.

Numerical Designations used in Part II.	Designation adopted in this Work.	Designations most commonly applied in the Past.			
		PISCES.	AMPHIBIA.	SAURIA.	THERIA.
No. 1a ..	Premaxilla. dermal part.	(+1) Premaxilla. Ascending process.	Premaxilla. Ascending process.	Premaxilla. Ascending process.	Premaxilla. Ascending process.
No. 1b ..	Premaxilla. Primitive mucosal part.	Prevomer.	Absent ?	Absent ?	Absent ?
No. 1+3	Premaxilla.	(+1) Premaxilla. Vomer.	Premaxilla.	Premaxilla.	Premaxilla.
No. 2 ..	Maxilla.	(+1) M a x i l l a. Palatine.	Maxilla.	Maxilla.	Maxilla.
No. 3 ..	Premaxilla. Palatine process.	(+1) Premaxilla. Palatine process. Vomer except tooth-bearing edge.	Premaxilla. Palatine process.	Premaxilla. Palatine process.	Premaxilla. Palatine process.
No. 4 ..	Palatine.	(+2) Ectopterygoid.	Palatine.	Palatine.	Palatine.
No. 5 ..	Ectopterygoid.	Pterygoid.	Pterygoid.	Ectopterygoid.	Absent.
No. 6 ..	Metapterygoid.	(+3) Metapterygoid.	Ectopterygoid.	Absent.	Absent.
No. 7 ..	Pterygoid.	Parasphenoid.	Parasphenoid.	Pterygoid.	Pterygoid.
No. 8 ..	Vomer.	Parethmoid and ectethmoid.	Prevomer.	Prevomer.	Prevomer.

(+1) Archaic fishes only.

(+2) Palatine in *Eusthenopteron*.

(+3) Pterygoid in *Acipenser*.

#### THE PREMAXILLA (Nos. 1a, 1b and 3).

This bone is believed to have been formed by the fusion of two or three elements, namely, those numbered 1a, 1b and 3. Originally, it is thought, all three were free from each other, as in *Latimeria* (Fig. 2). Although there is no definite evidence in the developmental history of the bone to support the belief that it was formed by the fusion of a dermal and a mucosal element in *Polypterus* (Fig. 4), there can be little reason to doubt that the canal organs in the ascending process indicate very definitely that, in this form at least, this portion of the bone is a dermal bone. The same evidence points to the same conclusion with respect to the bone in *Lepidosteus* (Fig. 5). The situation of the bone in *Eusthenopteron* supports this view, and in *Latimeria* there are dermal ossicles, closely resembling those of *Lepidosteus*, in the skin of the front of the mouth a short distance in front of teeth-bearing ossicles embedded in "the skin of the mouth" (Smith). It is undeniable that were 1a and 1b in *Latimeria* to fuse, we should have the condition of the bone in *Polypterus*, but with both parts quite small. The homology of the bone in *Amia* with that of *Polypterus* has not been, nor probably will it be,

denied. This equation has included the ascending processes of the two bones. The fact that one bone bears canal organs and is definitely a dermal bone, whilst the other does not, may be accounted for on the simple assumption that the bone in *Amia* has become submerged below the dermal mucosal layer. It has certainly grown further back and is much more extensive medially. On the other hand, in *Polypterus* the bone has acquired a much more extensive palatine lamina, this also probably by submergence and simple increased growth. The alveolar margin in both is planted upon the front edge of the ethmoid cartilage, and ascending and palatine processes have grown back in contact with the upper and lower surfaces of the cartilage.

Now, if one visualizes the features of the bones of *Polypterus* and *Amia* (Fig. 6) combined\* and their ascending and palatine processes united around the antero-lateral edge of the cartilage just a very little further back, one would be visualizing a bone which is an actuality in a large number of adult teleosts, and, moreover, which develops in the same way, as a membrane bone. The bone in question is, of course, that numbered 1b + 3, and is that which has been designated vomer and, lately, prevomer in these fishes. The question of the duality of origin of maxilla and premaxilla in *Polypterus* is discussed by de Beer (1937, p. 84). The question at issue, as seen by him and others, is whether bones separate from these in other fishes have been fused with them. For the purposes of the present discussion the identity of the dermal component is not of importance; the only question is—is there a dermal component? De Beer believes that the question would be solved by a study of the earliest stages of their development. Apparently, if they each arise from more than one centre of ossification, he would regard the question as answered in the affirmative; if not, in the negative. Since *Polypterus* is definitely a primitive fish, and it is recognized as such because it has retained primitive features in the adult, it is probable that if these bones are ultimately found to develop from several centres, the centres would be primitive features also. But, as de Beer points out (l.c., p. 503), plurality of centres of ossification cannot always be accepted as evidence that the bone so commencing represents an equal number of bones in an ancestral form. On the other hand, the absence of plurality of centres of ossification can be accepted as conclusive evidence that the bone has *not* developed phylogenetically from more than one bone, only if one is prepared to accept the recapitulation theory in entirety. Such an acceptance compels a belief that no phylogenetic stage can have been omitted from the ontogeny. Only one instance can be recalled where the absence of two centres of ossification is not accepted as evidence of origin phylogenetically from a single bone. This instance is particularly pertinent to the present discussion. The single "vomer" of the Teleostei has been accepted as the homologue of the paired "prevomers" of archaic fishes and other vertebrates. There has been a general agreement to ignore the general absence of any embryological evidence of duality of origin when weighed against other features.

Reviewing the evidence of the bones in the archaic fossils, in *Latimeria*, *Polypterus* and *Amia*, it appears entirely reasonable to believe that the premaxilla has been developed phylogenetically by the fusion of dermal and oro-mucosal bones.

Comparing the relations of the premaxillae of *Amia*, and particularly that of *Polypterus*, with the "prevomer" of the Teleostei generally, one cannot but be impressed by their *detailed* similarity. The embryology of the "prevomer" is not opposed to the view that it is homologous with the paired premaxillae. The "prevomer" always commences as a membrane bone, and only later, in some forms, becomes a perichondral ossification. (In *Salmo* the bone is paired anteriorly and the teeth are at first not attached to the bone.) In view of the fact that the departure from complete similarity in development, i.e., duality of centres of ossification in the one and not in the other, cannot be regarded as conclusive evidence, a decision must be made largely on adult relations.

The only reason that the "prevomer" of the Teleostei has not been recognized as homologous with the premaxillae of other fishes and the tetrapods is that the anterior

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\* The ascending process of *Polypterus* has no medial piece and is separated from its antimere by the mesethmoid.

lip bones have been identified as the premaxillae. But for this error the truth would have been recognized long ere this.

It is a peculiar fact that the identification of the lip bones as premaxillae has rested upon the single fact that they are located on each side in front of the mouth. It is a further fact that there is not one other single feature, either in their adult relations to other bones or in their developmental history, in which they resemble the true premaxillae. It is also a fact that neither the palaeontological record nor living animals or fishes present one single arrangement of the premaxillae which might be interpreted as an intermediate stage either in the process of liberation of the true premaxillae to form lip bones, or of partial fixation of the lip bones to form true premaxillae. Then, too, there is a perfect set of stages in the palaeontological record and in the living animals and fishes of the almost unaltered persistence of premaxillae such as those of *Eusthenopteron* or *Polypterus* throughout the whole series. Finally, during the metamorphosis of the tadpole, the absorption and final abolition of lip-cartilages, undeniably homologous with the lip bones of the Teleostei, may be observed. (Kesteven, 1942-44.)

It is concluded that the premaxillae of the Vertebrata have been developed by the fusion of dermal and oro-mucosal bones placed, the one in the skin of the lip, the other in the skin of the mouth, and that these bones early fused to form the single bone which soon came to be firmly bound to the anterior end of the cartilage of the snout, and that in the teleostean fishes the four labial cartilages became ossified to form a purely adventitious jaw anterior and lateral to the true jaws.

This account has neglected the bones numbered 1b in *Latimeria*, *Lepidosteus* and *Amia*, bones which have been designated prevomers in the past. It is believed that they are, in verity, simply dental plates of the premaxillae which have not fused with the palatine laminae of those bones. They will be discussed later in more detail.

#### THE MAXILLA. (No. 2.)

It is believed that this bone has been formed by the coalescence of two components. In *Latimeria* (Fig. 2) there are no separate "2a" dermal assicles comparable with the 1a series. It is possible that the tough matrix in the maxillary labial fold of this fish, noted by Smith, is a fibro-cartilaginous labial cartilage. In *Lepidosteus* (Fig. 5) and in *Polypterus* (Fig. 4) there is definite evidence that the ascending process of the bone is a dermal element, and repeatedly in the development of the bone in amphibian embryos, it is found to develop first in its ascending process and the palatine process develops later, either by extension from the alveolar ridge or as a separate centre of ossification. In archaic fishes and in labyrinthodont amphibians, the ascending process of the maxilla sutures with dermal shields, and is flush with the outer surfaces of the shields with which it sutures. It seems reasonably certain, from the condition in archaic fishes and amphibians, that the maxilla has been formed by the impressment of the peri-oral dermal shields and by increase in the size of the denticles along their ventral margins. The presence of a bone which may be confidently identified as a maxilla on the palatopterygoid of *Acipenser* (Fig. 1), and which cannot be regarded as a dermal bone, seems to indicate that, in this form at least, a maxilla has been developed from an oro-mucosal bone. In *Polypterus* the presence of a dermal component is beyond question, but the close association of the inner surfaces of the palatine process, alveolar ridge and ascending processes with the ethmoid cartilage, necessitates a choice between a belief in the simple extension of one primary element, or in the fusion of two primary elements to form the bone. The ultimate decision will be, even more than usual in these problems, a personal question depending on the weight of probability as each student sees it.

The identification of the maxilla in the Teleostei remains to be discussed. It is obvious that the "maxilla" of *Amia* is in no way homologous with that of *Polypterus*. There are no features of resemblance, except the presence of teeth, between the two bones either in respect to the adult form and topographical relations or to their embryological history.

On the other hand, the form and topographical relations of the adult "palatine" of *Amia* and maxilla of *Polypterus* are fundamentally identical, as also is their embryological history. If, in examining the evidence for and against the homology of these two bones,



each of the criteria listed on a previous page is used in turn, all support the equation. As against this conclusion, there remains only the established, but unfounded, conviction that it is correct to regard the labial maxilla as the true maxilla. That conviction is as wrong as it is unfounded. There is no doubt that the "palatine" of *Amia* is homologous with that of the Teleostei generally. The bone is, and should be, designated the maxilla.

#### THE PALATINE. (No. 4.)

Throughout the whole of the Tetrapoda the bone which has been designated palatine serves to bind the maxilla to median or admedian components of the maxillo-palate in the region of the nasopharyngeal canal and its posterior opening. With few exceptions the bone is structurally an important unit and contributes an extensive area to the bony palate. It is developed as a membrane bone in close relation to the ventrum of the lamina orbito-nasalis. In those forms in which the vomer or "preyomer" acts as a "corner-stone", strengthening the palate below the post-narial passages and connecting the palate to the skull, it is to this bone that the palatines are sutured medially. In some forms, e.g., crocodiles, cynodonts and Theria, the contact is along a median palatine suture. In the absence of the vomer as the central "stay" of the palate, the palatine bones are firmly sutured together in the mid-line, and are sutured to downwardly-projecting processes of the frontal bones. Only in the Urodela and Anura does the palatine pair of bones lose its importance as a structural unit of the maxillo-palatal arch.

In the fishes, the identification of the palatine bone in the archaic forms is not difficult. It has probably been correctly identified in *Eusthenopteron* (Fig. 3, No. 4) by Bryant and by Watson. In *Polypterus* it is fairly certainly the bone heretofore identified as the pterygoid (Fig. 4, No. 4). In *Latimeria* it is possibly the bone identified by Smith as the ectopterygoid (Fig. 2, No. 4). From *Polypterus* through *Eusthenopteron* to *Baphetes* and *Orthosaurus* and on to the saurians and therians, the same bone is traced with confidence.

The identification of the palatine in *Amia* and the Teleostei is far from a simple or straightforward matter. The palate of the Teleostei is peculiar in so many respects that one is forced to regard it as specialized, and then to try and determine how this specialization has affected its components. There are two outstanding features in this specialization. Firstly, the function of the true upper jaw has been transferred to the adventitious lip-jaw, so that it is this which opposes the lower jaw anteriorly instead of, as in archaic fishes and tetrapods, the true upper jaw. Secondly, the whole of the maxillo-palatal arcade has been made mobile on its long axis on each side to permit of that abduction and adduction which is so essential for gill respiration. These movements are effected by powerful adductor and abductor muscles, and areas for the insertion of these have been provided on the surfaces of the palatal bones, as well as for equally powerful "levator arcus palatini" muscles which lift the centre of the arch. In order to provide room for these muscles and their attachment, the whole of the arch on each side has been thrust from the centre line, and is set at an angle with the vertical sagittal plane to permit the respiratory movements to take place. Then, too, much of the sub-palatal area has been converted into an atrio-pharynx by the crowding forward of the branchial basket. Briefly, the whole structure subserves a respiratory function (not less important than that associated with feeding) which has called for freedom of movement of the whole upon the skull. This is met by articulation to the skull anteriorly as well as posteriorly instead of the rigid fixation which is seen in the tetrapods. The whole arch has been strengthened along its ventro-lateral margin, to take the pull of the "respiratory" muscles, and cast loose along the full length of the dorso-medial border to permit freedom of movement.

The bones which take so important a part in the fixation of the palate in front have either not acquired, or have lost, that function and are not so well developed.

It is believed that the bone in the teleostean palate which should be regarded as the homologue of the tetrapod palatine, is that which is numbered 4 in Figures 1 to 7. This is that which has been designated pterygoid and ectopterygoid in the past.

This identification is largely based upon an argument *per exclusionem* which will develop as the remaining bones are discussed.

## THE PTERYGOID. (No. 7a and 7b.)

This is the bone which has been designated parasphenoid in the fishes and euamphibians, and pterygoid in other tetrapods.

It is necessary to clear the ground of one outstanding error of identification in the past. There is no trace of a parasphenoid bone in any living saurian. In a search for the parasphenoid, Kesteven (1940) examined the osteogenesis of the basis cranii in twenty-six saurian embryos, representing every living group except the crocodiles and Rhynchocephalia, and demonstrated very conclusively that the small squame which had been observed on the ventrum of the basisphenoid cartilage of various reptilian and bird embryos was the outer table of the basisphenoid bone, and that this bone developed in the same manner as the basioccipital in every saurian embryo studied. This work was further confirmed for the avian bones in two later investigations (Kesteven, 1942a, 1942b), in which it was also shown that the "rostrum basisphenoidei" is an endochondral presphenoid ossification and not a membrane bone. Of course, it is known that there is no parasphenoid bone on the base of any therian skull.

There is then a truly remarkable difference between the saurian and therian skulls on the one hand and those of the rest of the tetrapods on the other, that is, if the large and functionally important parasphenoid is really not represented in the saurian skull.

This abrupt and complete shedding of an important structure is quite without parallel elsewhere in the fields of comparative osteology and anatomy.

Impressed by this, almost fundamental, difference in 1916, I sought to explain it away by proposing to regard the reptilian pterygoids as the two halves of the amphibian parasphenoid.

It is undeniable that there is strong resemblance between the "pterygoids" of the stegocephalians, especially such a form as *Eryops* (Fig. 11) and those of the Lacertilia (Fig. 28) and Ichthyosauria (Fig. 38), but this resemblance is purely superficial.

Comparison should not be made with conditions so specialized as those of reptilians in which the pterygoids are thrust away from the mid-line.

Commencing with the Sauramphibia\* and passing through the Cotylosauria (Figs. 20 and 21), Chelonia (Figs. 23 and 24), and Theriodontia (Figs. 33 and 39), there is a complete series of palates from the most primitive amphibio-reptilian and reptilian form to the saurio-mammalian form, in all of which the pterygoids meet in the mid-line, and which, moreover, do not appear to be specialized reptilian types. All of them may be regarded as occupying a place on, or close to, the main line, either back to the amphibian or forward to the therian condition.

If the pterygoid bones of any euamphibian be compared with those of *Baphetes* (Fig. 18), *Simosaurus* (Fig. 34), *Orthosaurus* (Fig. 19), *Seymouria* (Fig. 20), *Pareiasaurus* (Fig. 21), *Bauria* (Fig. 33), *Crocodylus* (Fig. 27) and *Chelone* (Fig. 23), it will be hard to find any features of true resemblance.

In every one of the amphibian forms the two bones are separated by the full width of the base of the skull, and this is covered by the parasphenoid. In all the reptilian forms the bones meet in the mid-line on the base of the skull, and there is probably no parasphenoid, certainly none in the chelonian and crocodile.

In the amphibians the pterygoid bone always extends forward and laterally around a subocular vacuity; this is never seen in any saurian.

The pterygoids in the reptilians always suture with the "prevomers" and with the palatines immediately on either side of the mid-line.

In the amphibians the pterygoids never suture with the prevomers and, if they suture with the palatine at all, it is on the outer boundary of the suborbital vacuity.

As illustrating how little real difference there is between the amphibian parasphenoid and the reptilian pterygoids, the condition in *Crocodylus*, cited by Kesteven, 1919, may be described again. Here there is, in the adult, one single triangular membrane bone with an anteriorly-projecting spur covering the basisphenoid. From this there stands forward

\* This term was introduced (Kesteven, 1942-44) to include those Amphibia, e.g., *Embolomeri*, which present the large "pterygoid" bones meeting in the mid-line, and which, it is agreed, were, or were closely allied to, the stock from which the Sauria were evolved.

and out on each side, a bone which supports the hinder end of the maxillary arcade (Figs. 26 and 27). The resemblance does not end here. Where this single bone projects beyond the basisphenoid, it carries the ventral surface of the presphenoid cartilage in a trough on its upper side. These conditions reproduce completely those of the amphibians. There can be no doubt that the ventral edge of the interorbital septum of such a form as *Trematosaurus* (Fig. 10) was lodged on the dorsal surface of the anterior process of the parasphenoid and, in recent amphibians, the presphenoid region of the skull-base rests on the bone.

There is little room for doubt that if this bone in *Crocodylus* had not developed subnarial laminae which meet in a median suture, it would have been identified as the parasphenoid bone, and it would have been regarded as a single bone until the embryologists demonstrated the presence of two centres of ossification in the early stages. Be that as it may, the fact remains that the only feature wherein this bone differs from the parasphenoid of the amphibians is that it develops from two centres of ossification. As a matter of fact, in the adult it is a parasphenoid.

We turn next to compare the amphibian "pterygoids" with those reptilian pterygoids which are thrust from the centre. For this purpose the pterygoids of such forms as *Eryops* (Fig. 11) and *Rhinesuchus* are selected because they resemble the reptilian condition more closely than others. The resemblance to the condition in *Pariotrichus* (Fig. 37) is superficially very close, especially if it be granted as possible that there was a parasphenoid on the base of the basisphenoid. However, more careful examination finds two important differences. The reptilian bones meet anteriorly, they are entirely medial to the palatines, and, finally, they suture with the prevomers. In lacertilian palates this last feature is not present (Figs. 28 and 29). As against the resemblances, it is not reasonable to assume the presence of a parasphenoid on the base of the basisphenoid in *Pariotrichus*. It is quite wrong to compare isolated examples from either group. The bone in *Eryops* has an extension forward which is not present in the great majority of other amphibians. The separation of the pterygoids in *Pariotrichus*, *Lacertilia* and Ichthyosauria is also a feature peculiar to just a comparatively few, specialized reptiles, and must be so regarded. It would be equally wrong to cite the condition in *Amphisbena* (Fig. 29) as a lacertilian form; it is probably one of the very few examples of a specialization which has taken the form of a more primitive condition. In this respect the condition in *Hyperodapedon* (Fig. 31) may be compared with the more specialized, well-known *Sphenodon*.

Turning next to the Sauramphibia, the pterygoids in *Baphetes* (Fig. 18) are readily equated with those of *Orthosaurus* (Fig. 19), and it is difficult to believe that the latter is not the homologue of the large bone in the palate of *Eusthenopteron* numbered 5.

When it is remembered that *Eusthenopteron* was a fish with hyoid suspension, one realizes that a lot of changes must have accompanied the alteration in the method of suspension, if the tetrapod maxillo-palate was developed by modification of one slung in that manner. On the other hand, it is probable that the tetrapod palate was evolved from that of a monimostylic ancestor and the hyostylic maxillo-palate only resembles the monimostylic because both have derived their bones from a common ancestor.

It is not difficult to believe that the freely hung hyostylic maxillo-palate of the *Acipenser* type became anchored, first after the manner of the Notidanidae, and then as in the Holocephali, and, finally, acquired the anchorage of the Dipnoi.

Such, in fact, appears to be the reasonable view to adopt. Otherwise, the incorporation of the covering of the base of the cranium into the bony roof of the mouth, and its very large share in that roof, is almost incomprehensible. In all the hyostylic forms the skull base takes little or no share in roofing the mouth, but in all the Euamphibia the parasphenoid is a very wide and expansive component. One should surely endeavour to visualize assumed changed topographical relations together with their probable mechanical changes or persistences.

Let it be assumed that the maxillo-palate, already fully formed and slung in the mobile manner of that of the hyostylic bony fishes, loses the anterior mobility about the ethmo-palatine junction, and, at the same time, it loses the hyoid suspension, the

quadrate being drawn in to become directly attached to the skull, and that the whole loses its respiratory function.

These changes will have taken place under the influence of a persistent need of an efficient masticatory musculature, a gradual abolition of the muscles which effect respiratory movements, or their transfer to other functions.

If this was the road the muscles of the mandibular and hyoid segments travelled in their modification from the elasmobranchian to the amphibian condition, some trace of the teleostean phase should become apparent on comparative study. As a matter of fact, one may trace the evolution of these muscles from the elasmobranchian directly to the amphibian condition, more than one stage in the process being manifest in the Holocephali. The teleostean condition presents one single instance of a muscle condition intermediate between the elasmobranchian and that of the amphibians. The facts are that one finds the muscles of the elasmobranchian fishes in the bony fishes, but in many respects very much modified. The same muscles are found also in the amphibians, and much less changed.\*

An obvious deduction from this evidence is that the cephalic musculature of the bony fishes is a specialization, and that it was not present in forms ancestral to the amphibians. The evidence of the muscular system supports the view that the amphibians have not passed through a teleostome stage. If the cephalic musculature is specialized, it is permissible to assume that it was specialized to adapt it to a special set of stresses and strains in a specialized framework.

The most primitive amphibians known to us are the Dipnoi. There is no doubt that they antedate the rest of the amphibians phylogenetically. So much so in fact that, although they possess so many amphibian characters, their possession of some very characteristic fish features has caused them, until recently, to be universally regarded as fish (Kesteven, 1931; Kerr, 1932).

Unfortunately, these primitive amphibians are extremely specialized in their maxillo-palatal features. There is no room for doubt that they have lost all the components of the maxillo-palate except those developed upon the base of the cranium. That which remains is of particular interest (Fig. 8).

The parasphenoid is a wide plate of bone essentially similar to that of the Euamphibia.

Here, then, is an exceedingly primitive amphibian, in fact, one may say, a pro-amphibian, and it is found to have the skull widened between the otic capsules, its base flush with that of those capsules, and with the basal process of the quadrate, and this wide expanse already covered by a wide parasphenoid which functions also as the bony roof of the hinder part of the mouth.

For the Euamphibia this may be taken as the primitive form of the central area of the roof of the mouth, and it indicates an origin for the palate of the Tetrapoda from a monimostylic rather than from a hyostylic form.

This is not the only significance of this extremely simple palate. On either side of the parasphenoid bone there is another which occupies precisely the situation of the pterygoid bones of those reptiles in which they meet one another anteriorly.

These bones are definitely *not* homologous with the pterygoids of the Euamphibia. They are developed quite differently. They are both membrane bones, but there the similarity ends. The bones in *Ceratodus* and *Lepidosiren* are developed in relation to the cranial base and extend from behind forward and medially; those of the amphibians, in relation to the palato-ptyergoid cartilage, and extend from behind forward and laterally. The location and development of these bones is such that they can be homologized only with the pterygoids of the reptiles.

If these two bones are not new ossifications making their first appearance on the base of the dipnoan skull, they should be recognizable as membrane bones on the lower part of the wall of the otocrane or alisphenoid region of the skull of fishes. In the search for this bone one would turn naturally to elasmobranchian types. Of these the Chondrostei are the only living forms which develop bones, and they provide nothing

\* It is not possible to give the details here; reference may be made to Kesteven, 1942-44.

comparable to this bone 7*b* in the Dipnoi. Nor is there any to be found in other fossil or living bony fish. It is, of course, possible that a precursory cranio-mural bone will be found in a fossil at some future time, but, at present, we are compelled to regard it as a bone not present in more primitive forms, that is, it must be regarded as a new bone.

But, if a new bone, it is not a cranio-mural element. It is possible that each of these bones has been developed from the osteogenetic stroma of the parasphenoid. In other words, it is not unreasonable to assume that these present us with the first stage in the replacement of the parasphenoid by two other bones each of which commenced as a separate centre of ossification of the parent bone; the writer believes this to be their history.

Whatever be the true explanation of their origin, it seems certain that they are the precursors of the pterygoid bones of the reptiles.

It must, however, be remembered that these are very definitely not homologous with the "pterygoids" of the Euamphibia.

It is probable that somewhere in the palaeontological record, further illuminating chapters in the history of the evolution of the palate, and especially of the pterygoid bones, will be found.\*

The occurrence in Carboniferous and Lower Permian times of such forms as *Seymouria*, *Pantylus* and *Pareiasaurus*, together with a variety of labyrinthodonts, indicates that a marked diversity of palates had already been evolved. Already in *Baphetes* a close approach has been made to the reptilian type.

One looks to the palaeontological record to provide stages intermediate between that of *Ceratodus* and the reptilian without any parasphenoid.

It is concluded that the pterygoid bone of the Sauria is not homologous with the "pterygoid" bone of the Euamphibia, but that it has been evolved by fragmentation and ultimate replacement of the parasphenoid bone.

#### THE ECTOPTERYGOID. (No. 5.)

Before discussing the homology of this bone as *between* the different classes, it is necessary to review each of the bones *within* the various classes. In the fishes, various names have been given to the bone; probably that most generally used is mesopterygoid. Whatever be its homologue in the tetrapod palates, it will probably be agreed that "No. 5" is the same bone in the fish palates illustrated (Figs. 1-7). Turning to the euamphibian palates, "No. 5" is the bone which has been designated pterygoid, and there is no room for doubt that it is the same bone which is so numbered in Figures 10 to 17. In the Sauramphibia and saurians the bone numbered 5 is that which has been designated as transversum and ectopterygoid.

The "pterygoid" bone of the amphibians is always developed in relation to the pterygoid portion of the cartilaginous palato-quadrate arch. It always appears first in front of the quadrate portion of that arch and its extension backwards follows later. Except in the coecilians the bone originates as a membrane bone. In some forms the cartilage remains, in others it may be actually replaced by endochondral ossification which fuses with the original membrane bone. In other forms the cartilaginous arch is simply absorbed without replacement. In the coecilians the bone is an endochondral ossification *ab initio*.

In the saurians the palato-quadrate arch never extends anteriorly beyond the basiptyergoid process sufficiently to provide a base in relation to which the ectopterygoid

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\* Price (1935) believed he found a parasphenoid, together with pterygoids, in *Captorhinus*, and White (1939) describes both bones in *Seymouria*. These may possibly represent a further stage in the reduction of the parasphenoid and its replacement by the true pterygoids. Careful investigation of the structure of the base of primitive saurian crania is needed to clear up this question. Sections may be expected to show a definite interval between basi and parasphenoid bones if both are present; and this interval should be visible—perhaps not continuously, but repeatedly—in most of the sections. Evidence of this kind will be necessary before the reported presence of a parasphenoid fused to a basisphenoid can be accepted. It must be remembered that there is no instance amongst living fish or amphibians of the parasphenoid being fused to any bone.

might arise. The bone always develops as a membrane bone. In view of the different modes of development of the bone in the amphibians, the absence of any relation to cartilage in the saurians cannot be regarded as evidence against the homology of the two bones, especially in view of the fact that the bone so commonly develops entirely as a membrane bone in the amphibians.

Since the facts of the embryology of the bones neither support nor oppose their homology, it becomes necessary to arrive at a decision by consideration of the adult relations in recent and fossil forms.

Superficial comparison of the "pterygoid" of the labyrinthodonts with the ectopterygoid of the saurians would lead at once to the rejection of the equation proposed here. An analysis of the relations of the two bones must, however, cause hesitation. In the labyrinthodonts the bone intervenes between the basis cranii and the articulation of the quadrate thereto on the one side, and the maxillary arcade on the other. Medially the bone sutures with the "parasphenoid"; laterally and anteriorly it sutures with the bone designated "ectopterygoid" when that is present, and in its absence, with the posterior end of the maxilla and/or the palatine. The suture with the "parasphenoid" is constant throughout the amphibians. In coecilians it sutures only with the palatine laterally and anteriorly. In *Urodeles* the bone is commonly much expanded, recalling that in *Batrachosuchus*. In the majority of the Urodela the bone ends short of the maxillary arcade. When it reaches the arcade, it sutures with the maxilla. In Anura the conditions are essentially as in the labyrinthodonts, but the bone is much more slender, and there is no "ectopterygoid" present; the anterior suture is with the maxilla.

The ectopterygoid of the Sauria\* makes a much smaller contribution to the maxillo-palate than does the "pterygoid" of the amphibian. It is commonly a small, sometimes a very small, bone sutured to the pterygoid medially and to the palatine and/or the maxilla laterally in front. If, as contended in the last section, the pterygoid is the homologue of the parasphenoid, the relations to other bones are as in the amphibians. In the great majority of the amphibians the "pterygoid" is so much larger than the ectopterygoid of the saurians that it is difficult to believe that they are homologous. Consideration of the other features in the maxillo-palate leads to a better understanding. In the majority of the amphibians the lateral margin of the "parasphenoid" is separated a long way from the inner margin of the maxillary arcade, and the bone which acts as a strut from the base of the cranium to the arcade is necessarily long and relatively stout. In the coecilians the base of the cranium and its investing parasphenoid is relatively much wider than in the rest of the euamphibians and, moreover, the maxillary arcade is not set so far away. The "pterygoid" bone is markedly reduced. This reduction of the bone is also observed throughout the saurians and Sauramphibia. The pterygoid bone in the Sauria is either very extensive with a wide anterior as well as posterior expansion, or else, as in the lacertilians and ophidians, it is a long narrow bone removed well away from the mid-line and supported near the middle of its length by the basiptyergoid process medially and the epiptyergoid superiorly. In the result, the gap between the pterygoid and the maxillary arcade has been markedly reduced, as in the coecilians, and, as in those amphibians, the ectopterygoid is also reduced. The smaller the gap the smaller the ectopterygoid. Probably the saurian condition which most nearly reproduces that of the Euamphibia is that of the Crocodilia (Figs. 26 and 27). In these forms the pterygoids are confined to the primitive position on the ventrum of a relatively narrow cranial base. The ectopterygoid is tripartite. The largest of the three processes runs forward and laterally to the maxillary arcade, the smallest is sutured to the side of the pterygoid, the third runs back to suture with the quadrate and prootic bones.

The nearest approach to the saurian condition in the Euamphibia is, of course, that of the Coecilia.

In the Chelonia the pterygoids are so wide and so long anteriorly that they suture with the palatine anteriorly and also with the maxilla.

\* There is no trace of the bone in any avian maxillo-palate.

It appears certain that if the "pterygoid" bone of the Euamphibia is represented in the palate of the fishes, it is by either bone No. 5 or No. 6. As already stated, there is reason to believe that the palates of both tetrapods and fishes owe their resemblances to the fact that both have inherited the bones from a common ancestor. Any investigation into the homologies of bones in the two types of palate should not, if the above belief be well founded, take the form of an enquiry as to how bones of the fish palate could have been modified to assume the form and relation of bones in the tetrapod palate. Just as it was found possible to trace the evolution of both teleostome and amphibian cephalic musculature from the elasmobranchian, so should the attempt be made to explain the two types of palate without assuming that the fishes present a phase in the evolution of the tetrapod.

The bone numbered 5 in the fish palates is a large bone in every case, and it is particularly significant that it is the largest bone in the palate of *Acipenser* (Fig. 1). The position of this bone is such that if the palato-quadrate passed through the notidanid and holocephalan stage to the condition of the dipnoan, and the bone persisted in its relation to the posterior end and ventral surface of the palato-ptyergoid cartilage, it must have come to occupy the situation of the "pterygoid" bone of the euamphibian palate. As a matter of fact, this line of reasoning leads us to the accepted belief that the large bone on the median side of the fish palate is the homologue of the amphibian pterygoid.\*

There remains one bone in the fish palate for which the homologue in the tetrapod palate has yet to be found. The metapterygoid is apparently not represented in the tetrapod palate, unless the "ectopterygoid" of some of the labyrinthodonts is its homologue. There is nothing in its topography or development in the living fishes to oppose this identification. But it should be designated metapterygoid in order to prevent confusion with the true ectopterygoid of the reptiles, which, it has been shown above, is the homologue of the euamphibian pterygoid.

#### THE VOMER. (No. 8.)

Parrington and Westoll (1940) reviewed the evidence in support of the equation of the therian vomer with the anterior part of the parasphenoid, and demonstrated fairly conclusively that the evidence in favour of equating the bone with the prevomers of the reptilian palate heavily outweighed it. They did not, however, investigate the origin of the prevomer.

This, like other problems discussed in the previous pages, will be approached without any assumption that the tetrapod vomer has been evolved by the modification of the vomer of the fishes.

Reviewing again the postulated stages in the anchoring of the palato-quadrate to the skull, the first stage was the firm fibrous union of the anterior end of the palato-ptyergoid cartilage to the ethmoidal cartilage in front of the orbit. Later there may have followed the complete fusion of the cartilages, as seen in the Holocephali. This union took place at the side of the ethmoid cartilage, the "symphysis palato-quadrate" was abolished, and the fore ends of the two cartilages came to be separated by the width of the ethmoid mass.

At the same time the dermal scutes surrounding the mouth fused with the oromucosal premaxillae and maxillae, and with the loss of the fore parts of the palato-ptyergoid cartilages, these bones acquired a direct relation to either the ethmoid cartilage or to the bones developed thereon. Thus, it may be supposed, the tetrapod maxillo-palate became firmly attached to the skull in front. In the bony fishes the process was very similar, but the retention of the gills and the need for respiratory movement prevented the development of complete immobility. The union in front

\* It is now possible to conclude the argument *per exclusionem* by which the identity of the palatine bone in the fish palate is identified.

With only two bones, Nos. 4 and 5, from which to select, it is obvious that the choice must fall on the anterior of the two, that which has been designated the ectopterygoid, as the palatine bone of the tetrapod palate. It will be noted that this is in agreement with the identification of the palatine in *Eusthenopteron* (Figs. 3A, 3B) by Bryant and Watson.

was by a firm joint about which a limited but definite amount of movement was possible. In both fish and tetrapod the true premaxillae were developed in relation to the front of the ethmoid cartilage, and the maxilla in relation to the side of that cartilage and to the fore end of the palatine process.

In the fishes the ethmoid mass of the skull remains solid, but in the tetrapods the ethmoid mass was excavated to contain the nasal organs, and the cartilaginous floor had to be strengthened by bony plates; these plates are the prevomers.

The prevomers are membrane bones, and are developed on the ventrum of the ethmoid cartilage. They suture with palatine plates of all the bones they contact.

In the fishes the only bones which appear to satisfy this definition are the prevomers of *Amia* and *Lepidosteus*. The former are placed superficially to the palatine laminae of the premaxillae, and those of the latter are altogether too much specialized to be safely used in the present comparison. The prevomers of *Polypterus* are definitely and completely separated from the ethmoid cartilage by the palatine laminae of the maxillae and premaxillae, and by the ectethmoid. No one of these is sutured to surrounding bones.

The bone in the Teleostei which has been termed vomer is so much more like the premaxillae that it is not possible to regard it as other than that bone.

The relation of the prevomers of *Eusthenopteron* (Figs. 3A, 3B) and other fishes to the ethmoid cartilage is unknown; their location leads one to believe that they are homologous with the bones in *Amia* (Fig. 6) and *Polypterus* (Fig. 4).

Apparently there are for comparison with the tetrapod prevomers only bones in two living fishes and, perhaps, similar bones in some fossils, and those in the recent forms are definitely placed more superficially in the tissues below the cartilage than are the tetrapod bones, nor do they make sutural union with any other bones.

In the tetrapods there is nothing to represent the ectethmoid. This is the bone through which the maxillo-palatal arch is anchored to the skull in the fishes. It is also the bone which ossifies the orbito-nasal lamina in the fishes.

The only bone in the tetrapods which ossifies on the orbito-nasal lamina is the prevomer.

The ectethmoid always develops as a perichondral ossification, with extensions in membrane in some forms.

The prevomer always develops as a membrane bone in the saurians, but appears to be a cartilage bone in some therians.

If there be strong reasons for believing that the prevomer and the ectethmoid are homologous, their different modes of development should not be permitted to weigh too heavily against the belief. There are numerous instances of bones, undoubtedly homologous, developing as cartilage bones in some forms and as membrane bones in others.

It is believed that the prevomers and the ectethmoid bones are both derived from the osteogenetic stroma which gave rise to ossification on and around the postero-lateral part of the ethmoid cartilage; in view of their different positions, one hesitates to advocate that the name prevomer be applied to the ectethmoid.

The problem is somewhat similar to that of the correct name for the derivatives of the hyoid superficial constrictor sheet of muscle fibres of the selachian. It is fairly certain that the posterior belly of the digastric muscle of the Theria is derived directly from the depressor mandibulae of the Sauria, and both from the selachian sheet, but, owing to changed form and function, one hesitates to designate the latter "posterior digastric". In this instance, there is strong reason to believe that the two bones are derived from a common precursor, but it does not seem advisable to bestow the same name on them.

In the study of the evolution of muscles it is possible to trace the gradual metamorphosis of a sheet of constrictor muscle fibres into separate entities, each having a new function. One is able to visualize the manner in which these fibres have been made use of in the presence of changing mechanical factors, their origins and insertions moving just a little, now forward, now back, to bring about greater range and/or efficiency of movement, or greater stability in a changing skeletal framework.



This concept of the control of anatomical units by changing mechanical needs is now brought to the study of the evolution of the maxillo-palate, and applied to the changes believed to have taken place in the bones under discussion.

The outstanding mechanical need in the particular region we are discussing was the firm attachment and, finally, immovable fixation of the anterior end of the arch to the anterior end of the skull.

There is little doubt on the evidence before us that this was not merely a *constant* factor in the mechanics of the structural evolution of the maxillo-palate, but was a *constantly increasing* factor. This is borne out by the fact that the anterior part of the skull and the maxillo-palate have become intimately, and very firmly, bound together, whereas there is no doubt, primitively, the arch was not bound to the skull anteriorly at all; it was loosely hung beneath it.

With this factor well in mind, it will probably be readily admitted that once the arch became firmly bound to any bone investing the postero-lateral corner of the ethmoid cartilage, the bone would continue to function as the point of attachment. Once the attachment had been effected, it is to be presumed that it would have become the permanent one.

There is no apparent reason why it should be assumed that the perichondral ossification should disappear altogether and part at least of its situation and its function be taken up by an entirely new bone. This last assumption is implied by the belief that there is no ectethmoid bone in the tetrapod skull, in view of the fact that the prevomer occupies the situation of the ventral part of that bone.

As stated before, the prevomer is the only bone which is ossified on the ventrum of the lamina orbito-nasalis. Of course, the maxilla and palatine bones both develop beneath the lamina orbito-nasalis in certain amphibians, but it is quite impossible to regard either of them as homologous with the ectethmoid, which is present with them in the fishes.

The topographical features of the prevomers are not the only characters which lead to their identification as being derived from a parethmoid ossification. They are the bones by which, in the Amphibia, the fore end of the maxillo-palate is knit to the skull, and by which the two halves are bound together.

It is significant that in very many teleosts a small area of the ventral surface of the ectethmoid bones presents in the palate between the arch and the mid-line, and that in this situation they commonly make sutural contact with the tip of the parasphenoid and nearly meet in the mid-line.

In all these features this portion of the bone resembles the prevomers of the amphibians.

As throwing light upon the evolution of the structure of the therian palate, it is of particular interest to note that the prevomers retain the function of acting as the main support of the palatal arch. In the chelonians this is very striking, is little less so in the cynodonts, and is still well in evidence in the Theria.

The migration of the bone from the side to the centre of the palate has apparently taken place without any break in the continued rigidity of the fixation of the arch, and also apparently in order to provide for the necessary support of the middle of the palate caused by the cavitation of the ethmoidal region for the accommodation of the increased size of the nasal passages, both in front and behind the nasal organ itself.

It is concluded that there are strong reasons for believing that both the ectethmoid and the prevomer were derived from the same parethmoid ossification, and that they should be regarded as homologous bones.

Of the two forms the ectethmoid is probably the more primitive.

It is believed that the "prevomer" of *Amia* (Fig. 6, 1b), *Polypterus* (Fig. 4, 1b), and the fossil archaic fishes are simply laminae formed by the fusion of the bones of the teeth they bear, and that they may be represented by the tooth-bearing portion of the premaxillae in teleosts. They are primitive 2b ossifications which may or may not be intimately fused with the palatine laminae.

Parrington and Westoll have practically demonstrated that the mammalian vomer is derived from the "prevomers" of the Reptilia. The following brief remarks are offered in support of their demonstration.

Slightly modified in the region of the "ectopterygoid" (5) to include features present in the majority of the Cynodontia, their illustration of *Cynognathus* is reproduced here (Fig. 39).

There is no reason to doubt that the vomer of *Cynognathus*, and of the Theriodontia, is homologous with the "prevomers" of the Chelonia, Crocodilia and Reptilia generally. These bones are not derived from the parasphenoid.

The fundamental similarity of the cynodont palate to that of the Theria is obvious, at least as far back as the posterior limit of the vomer.

If the vomer of the therian palate is not the same bone as the cynodont vomer, then it must be assumed that the central strut of the palate, an essential structural unit, was replaced with identically the same relations to all the other units, by a new bone—an altogether unnecessary and an unreasonable assumption.

It is concluded that the therian vomer is the same bone as the reptilian "prevomer", and the latter name should be discarded.

#### THE EPIPTERYGOID.

This name has been given to the "metapterygoid" bone in the fish palate by several palaeontologists in recent years. Parrington and Westoll, in their very careful review of the evidence bearing on the evolution of the mammalian palate, follow the palaeontologists in adopting this very misleading and erroneous name for the bone.

The name "epipterygoid" was applied for many years to the bone which Owen and Huxley designated *columella cranii*, and to this bone only. It has been demonstrated, as conclusively as such things can be demonstrated, that the lacertilian epipterygoid is the homologue of the *processus ascendens quadrati*. This demonstration has gone unchallenged; it has been accepted by every comparative anatomist.

Unfortunately Gregory, and others, made the mistake of believing that the alisphenoid bone of certain cynodont reptiles was homologous with the epipterygoid of the Rhyngocephalia and Lacertilia, being misled in this matter by Gaupp's theory of the inclusion of a "cavum epiptericum" into the cranial cavity of the Theria. This theory was based upon the relations of certain nerves to the epipterygoid bone. Kesteven (1918) demonstrated quite conclusively that those relations were so variable as to be quite unreliable. Gregory and Noble (1924) accepted this evidence, but because the "epipterygoid" of the cynodonts was demonstrably homologous with the alisphenoid of the Theria, assumed that the epipterygoid of the lacertilians must be also. Kesteven (1926, 1941) demonstrated by the citation of embryological evidence and adult relations of the bones in fossil and recent forms, that the bone located in the alisphenoid region of the cranial wall in all living vertebrates is developed in essentially the same way (as a primary component of the cranial wall), that the relation of the bone to surrounding bones was constant, and that the same variations to soft structures (nerves and blood-vessels) which had been recorded as *between* the therian and saurian bones were also found, both in embryonic and adult conditions, with respect to the bone *within* both groups.

Gaupp's "cavum epiptericum" is definitely a myth (Kesteven, 1941).

The "epipterygoid" of the cynodonts was correctly named alisphenoid by Broom in his original descriptions, and since it is homologous with the alisphenoid of the Theria, it should be so named.

The epipterygoid of the Rhyngocephalia, Chelonia, Lacertilia and Ophidia\* is the homologue of the *processus ascendens quadrati*.

In all living amphibians, including the very primitive dipnoans, the quadrate is attached by ascending, basal and otic processes. (In *Coeilia* the ascending process only is present). It must be concluded that this method of attachment has been inherited by

\* In the Ophidia there is a bone which has *every one* of the relations to blood-vessels and nerves which are possessed by the therian alisphenoid, and are said to distinguish that bone from the bone in the Sauria, but because this is a saurian, the protagonists of the "cavum epiptericum" theory have refused to recognize it as an alisphenoid.

all from a common ancestor. It follows that the same form of attachment was, in all probability, present in the labyrinthodonts. The alternatives are two in number. Firstly, these amphibians did not have an ancestor in common with recent forms. Secondly, these amphibians were peculiarly specialized in *this one respect*. Neither of these alternatives is acceptable; neither is reasonable.

It must be concluded, therefore, that even if Gaupp's *cavum epiptericum* theory, with its attendant equation of the epipterygoid with the alisphenoid, were correct, there could have been no separate epipterygoid in the early amphibians.

Now, under the impression that the metapterygoid of the fishes could be homologized with an alisphenoid-like ossification (designated epipterygoid) in certain labyrinthodonts, Watson, Stensio, Sève Söderbergh, and other palaeontologists, have designated this bone epipterygoid also.\*

#### CONCLUSIONS.

Reviewing the foregoing discussions, perhaps the most outstanding feature of them all is the paucity of factual evidence available. Every one of the conclusions arrived at is an opinion based upon the interpretation of evidence largely circumstantial. But whilst, therefore, no one of these conclusions may be regarded as having been *established*, it is confidently believed that they present the most *reasonable* interpretation of the evidence.

In brief, those conclusions are:

1. The tetrapod maxillo-palate and that of the bony fishes have been evolved from that of a common ancestor.
2. The tetrapod maxillo-palate was not evolved by modification of that of the bony fishes.
3. In the fishes and the Tetrapoda alike the premaxillae and the maxillae were evolved by the coalescence of dermal ossicles in the skin of the lip, and oromucosal ossifications in the skin of the mouth, and that these bones very early became related to the front and lateral edges and contiguous ventral surface of the ethmoid cartilage.
4. In the Teleostei these two bones are those which, in the past, have been known as the vomer and palatine bones respectively.
5. As a result of the past misinterpretation of these two bones the whole of the bones in the maxillo-palate of the Teleostei have been misinterpreted also. Their correct homologies appear to be as set out in the table of nomenclature given on page 76.
6. The most primitive maxillo-palate in the Tetrapoda is that of the great majority of the Amphibia: the type characterized by the presence of a large parasphenoid bone.
7. In the Sauria and the Sauramphibia the median parasphenoid bone has been replaced by two bones which have been developed by fragmentation of the parent bone.
8. The earliest stage in this replacement is to be seen in the Dipnoi.
9. The prevomers of the Tetrápoda have been evolved from the ectethmoids (or parethmoids) of the fishes. It is believed that these bones were present in the common ancestors of both bony fishes and tetrapods.
10. The prevomers of the Amphibia and the Sauria are believed to be homologous with the vomer of the Theria.
11. The bone known in the past as the pterygoid in the Amphibia is believed to be the homologue of the ectopterygoid of the Sauria.

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\* The most astonishing extension of this misnomer is that at least three of the palaeontologists have found "basal", "otic", and "ascending processes" attached to this "epipterygoid", which if correctly named, is itself the ascending process of the quadrate. One wonders did these palaeontologists believe that the quadrate in these amphibians had the usual ascending, basal, and otic processes, and that from the ascending process, secondary ascending, basal and otic processes were developed, or was it just careless use of established designations with entirely new meanings?

12. The pterygoid bone of the Sauria is believed to be the homologue of the pterygoid of the Theria.
13. The "epipterygoid" of certain cynodonts is believed to be homologous with the alisphenoid of the Vertebrata generally, including that of the Theria, but *not* with the epipterygoid of the Lacertilia and some few other reptiles.

## PART II.

The following illustrations and brief descriptions supplement statements of fact in Part i. It would have seriously interrupted the presentation of the arguments if the descriptions had been given in Part i, but since the whole of the facts cannot be carried in the mind, it was felt that they should be made available. Several of the bones which have been regarded as homologous in the preceding pages have been known under different names in the different groups, and within the groups have been given different names by different workers. In order to avoid overloading the text with a conflict of nomenclature, numbers have been used instead of names for the bones. The key to the numbers will be found on page 76.

### (A). THE FISHES.

#### *Acipenser.* (Fig. 1.)

The quadrato-palatal arch is hyostylic and is not articulated or firmly bound to the skull in front. Anteriorly and laterally the maxillo-palate is firmly bound to the skin. This is rendered relatively rigid by the ossicles with which it is so richly endowed; in effect, this fixation in the skin of the snout gives that fixation which is obtained in some elasmobranchs and in the bony fishes by articulation to, or firm union with, the ethmoid cartilage.

There are five bones related to the palato-quadrato cartilage. Two of these, 1*b* and 2*b*, fuse very early to form a narrow splint which lies along the ventro-lateral edge of the arch, is in contact with the cartilage at both ends, but is separated from it between these points.

The largest of the remaining three bones is No. 5; this covers a large part of the ventro-medial surface as well as a smaller area on the dorso-lateral surface of the cartilage.

Numbers 4 and 6 are small bones applied to the ventro-medial edge of the cartilage.

Bones 3, 7*a* and 8, which are actually or potentially components of the maxillo-palate in all the fishes, are present on the skull of *Accipenser*, but take no part in the formation of the maxillo-palate. It is important that it be remembered that they are present on the skull.

#### *Latimeria.* (Fig. 2.)

The maxillo-palate is anchored in front to the ectethmoid, so that the palato-pterygoid arches are separated anteriorly, and the bones 8 and 7 appear in the roof of the mouth between them. Posteriorly the suspension is hyostylic, but this attachment to the skull is strengthened by the firm fibrous union of No. 6 to the prootic bone.

No. 1*a* is a series of dermal scutes in the skin of the lip on each side of the mid-line. No. 1*b* is a single ossicle in the skin of the mouth on each side of the mid-line just behind 1*a*. It is not planted on the ethmoid cartilage but lies very close to, and below, the anterior edge thereof. There is no labial sulcus between 1*a* and 1*b*.

No. 8 is a solid bone firmly attached to the postero-lateral corner of the ethmoid cartilage. Its ventral surface presents in the palate in front of No. 7*a* and medially to No. 3 it sutures with the front end of No. 7*a*.

No. 3 may be a separate bone or may be the anterior portion of No. 2. It is a flat plate of bone applied to the ventrum of No. 8 and sutures with the antero-medial edge of No. 2.

No. 2 is a more extensive and much stouter bone which sutures with the postero-medial part of No. 8 in front, lies below and medial to the anterior tip of No. 5, and is itself overlain ventrally by the anterior tip of No. 4.

Bones 2, 3 and 4 carry teeth along their lateral margins.

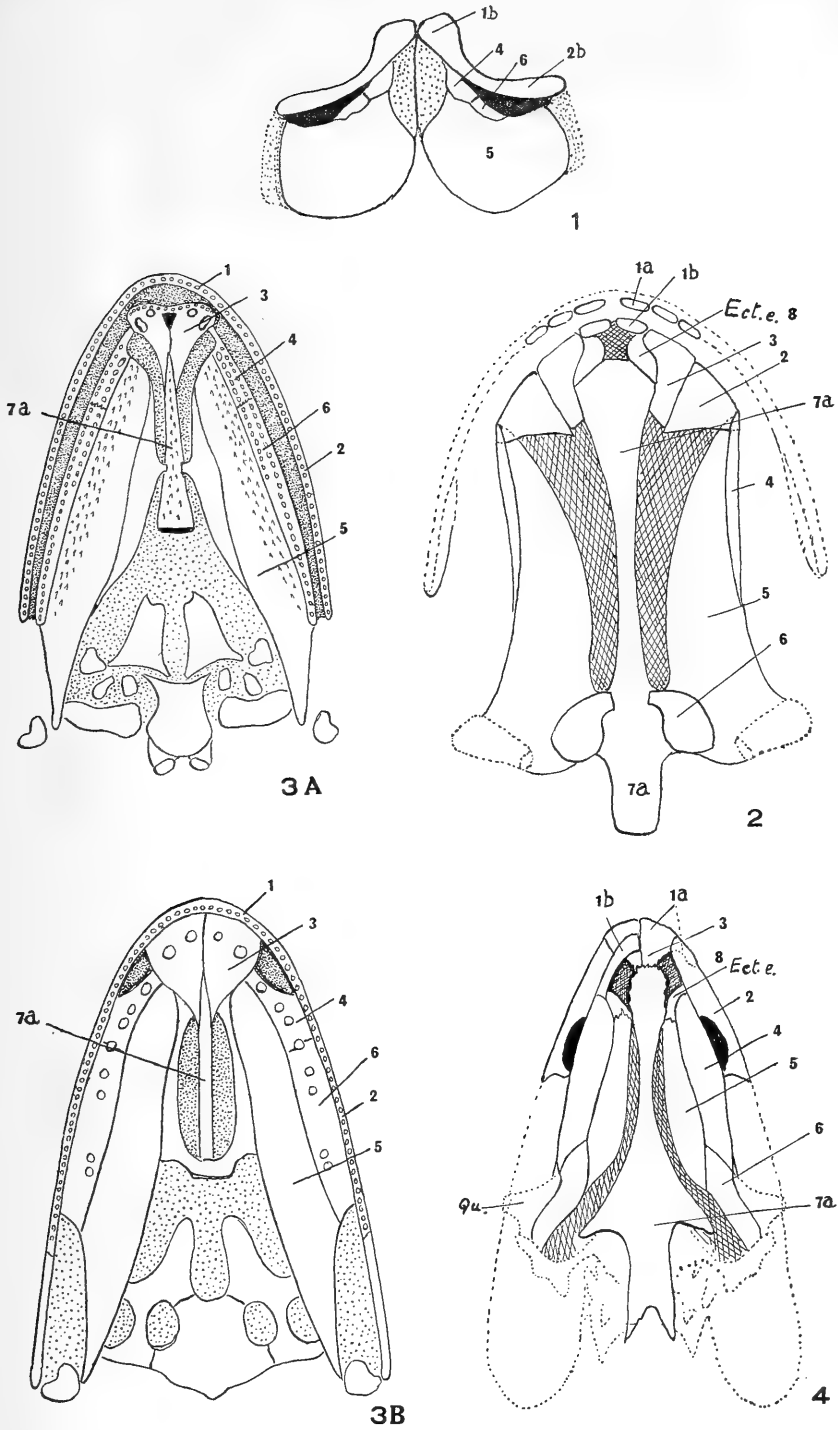


Fig. 1.—*Acipenser* (from Parker).  
 Fig. 2.—*Latimeria* (from Smith).  
 Fig. 3A.—*Eusthenopteron* (from Bryant).  
 Fig. 3B.—*Eusthenopteron* (from Watson).  
 Fig. 4.—*Polypterus* (from Traquair and Allis).

No. 4 is a splint bone sutured to the anterior half of the ventro-lateral margin of No. 5, but is separated from that bone at the extreme anterior tip where No. 2 is placed between them.

No. 5 is a much broader bone than it appears in the illustration; its width and also that of No. 6 is foreshortened. This is a relatively strong plate of bone and it is further strengthened by three thickened, radiating columns. The bone is triangular in outline with three unequal sides, the ventral side is the longest, and the posterior, nearly vertical, the shortest. The apex of the triangle is drawn out into a short process. The postero-ventral corner of the bone has the quadrate firmly united to it.

No. 6 was described by Smith as resembling a broad-bladed, short-handled cleaver in shape. The bone is very firmly sutured to No. 5, especially along the process rising from the apex of that bone. The angle between the "blade" and the handle is filled in to produce a curved edge, which is thickened and firmly bound to the prootic. The tip of the handle is close to the alisphenoid.

No. 7a has been broken off at the position of the dotted line across the bone, the portion shown behind this line being a "restoration" based on the extent of the bone in all other fishes.

There is, of course, only one specimen of this fish known. The illustration and above description are based upon Smith's description and illustrations. Dr. Smith has very kindly checked these for me, and I have to thank him for his assistance. I have not ventured to ask him to support my restoration of the posterior part of bone No. 7a.

Smith was particularly impressed by the absence of "premaxillae" and "maxillae". He described and illustrated a lip fold which resembles remarkably closely that in which the "maxilla" of the Teleostei is lodged. In the teleosts the fold is continuous right around the snout with that of the other side. The anterior part of the fold encloses the "premaxilla". This part of the fold is not present in *Latimeria*. There is a strong resemblance to *Amia* but in that fish the "maxillary" fold contains the "maxilla".

*Eusthenopteron*. (Figs. 3A, 3B.)

The maxillo-palate of this fish was described by Bryant (1919) and by Watson (1925). Both their illustrations are reproduced.

Numbers 1 and 2 are narrow, tooth-bearing bones with ascending laminae, doubtless sutured to dermal shield scutes. According to Bryant, there was an interval between these two and the rest of the bones of the palate, but Watson did not believe this to be correct.

No. 3. If Bryant was correct this triangular plate of bone had a row of teeth set along the anterior margin and a few larger teeth on the rest of the surface. Watson did not find the anterior row of teeth. Anteriorly the pair of No. 3 meet in a median suture but posteriorly they diverge and the anterior tip of 7a fits between them.

No. 4 is a narrow oblong bone sutured to No. 5 medially and perhaps to No. 2 laterally.

No. 6 is similar to No. 4 and placed behind it.

No. 5 is an extensive flat bone which had No. 9 attached to its median edge and was firmly sutured to Numbers 4 and 6 along its lateral edge. Posteriorly, the bone was probably firmly attached to the quadrate.

No. 9 was so fragmented in the specimens studied that the two observers differed a good deal in their interpretation of the fragments. It is possibly merely displaced fragments of skull bones.

*Polypterus*. (Fig. 4.)

1a is a relatively solid bone; it presents an alveolar margin beset with teeth, a palatine process and an ascending, dermal, process above the alveolar margin, applied to the ethmoid cartilage and articulating with the nasal, the lacrymal and No. 2. The palatine lamina is triangular in outline, it is planted directly upon the ventrum of the ethmoid cartilage, and sutures with 7a and 8. This palatine lamina is partly covered ventrally by the anterior portion of 1b, which is firmly bound to it, but is not actually sutured to, or fused with it.

1b is a curved flat narrow plate of bone which is bound to the ventral surfaces of the palatine laminae of Numbers 1a and 2.

No. 2 is a more solid bone than 1a. It presents an alveolar ridge, a dermal ascending process and a narrow palatine lamina. Anteriorly the ascending process is covered by certain of the dermal scutes, but posteriorly it comes to lie more superficially and, like the ascending process of 1a, it carries canal organs. In front, No. 2 sutures with 1a. The palatine lamina is sutured to No. 4 in two places.\* Laterally to the anterior of these two points, No. 2 is firmly bound to No. 8. In the cheek the posterior part of the ascending process sutures flush with dermal cheek plates.

No. 3 is, of course, the palatine process of 1a. It has been numbered for comparison with the greater part of No. 3 in the Teleostei.

No. 8 is a solid, approximately tetrahedral block of bone which is attached to the postero-lateral corner of the ethmoid cartilage. The ventral surface of this bone is covered in part by the palatine process of No. 2 and the anterior ends of Numbers 4 and 5 which are very firmly bound to it. The remainder of the ventral surface presents medially to No. 2 between that bone and No. 7a, and is just in front of Numbers 4 and 5.

No. 4 is an elongated flat plate of bone applied directly to the palato-quadrate cartilage. It covers the outer edge and lower, inner, surface to a large extent and the upper, outer, surface to a lesser extent. It is sutured to No. 2, as already described, is firmly bound to the ventral surface of No. 8, is sutured to No. 5 along nearly the full length of its medial edge and posteriorly it is sutured to No. 6.

Numbers 5 and 6 are also flat bones planted upon the palato-quadrate cartilage. They are firmly attached to one another and to No. 4. No. 6 is also firmly attached to the quadrate.

*Lepidosteus.* (Fig. 5.)

The very marked elongation of all the bones in this maxillo-palate, except No. 1, in front of the basisphenoid region of the skull, imparts to the whole an apparent dissimilarity with other fish maxillo-palates. The dissimilarity is due essentially to the elongation of the bones and not to fundamentally changed positions.

Whilst the hyomandibula still functions as one of the "slings" of the maxillo-palate, the whole of the bones are so closely built together, to the dermal shields of the much elongated snout and to the base of the skull, that it is now almost functionally redundant and is reduced in size.

No. 1 is a dermal ossicle with a narrow alveolar margin beset with teeth, and with no obvious palatine process. The ascending process carries canal organs.

No. 2 is composed of a numerous series of dermal scutes inseparably fused at their contactual margins but showing closed suture lines. Each is beset on the alveolar margin with small teeth and each has a narrow palatine process which is firmly sutured to the lateral edge of No. 4. The dermal scutes all carry canal organs. The canal in which these are lodged is continuous from scute to scute along the full length of the composite bone. Dorsally bone No. 2 sutures with dermal scutes of the snout.

No. 4 is a long, narrow, thin splint which extends from No. 1 in front, back along the full length of No. 2 and then a little further. Its medial edge sutures with No. 3 for about one-half its length and for the rest with the lateral edge of No. 5.

No. 3 is similar to No. 4 but narrower and nearly as long; it sutures with its antimer in the mid-line, and along its outer edge with Numbers 4 and 5.

No. 5, as in the other palates reviewed, is the largest bone of the series. Like the other bones in this palate, it is long and narrow. Anteriorly its lateral margin sutures with No. 4. Behind that bone the lateral edge of the bone is free. The median edge sutures with No. 3 anteriorly and with No. 7a behind that for some distance, and then with the outer edge of No. 6. This last is quite a small bone placed between Numbers 5 and 7a near the posterior end of 5.

\* The gap between this bone and No. 4 between these two points of suture is very similar to the gap between the front end of No. 4 and 2 in *Eusthenopteron* which palaeontologists believe may have been an internal naris.

No. 7a contributes relatively extensively to the median portion of the palate from two-thirds of the way back from the tip to the posterior end.

No. 8 does not appear in this palate at all.

Apart from the extraordinary length of this maxillo-palate its most outstanding feature is that the admedian bones are firmly attached to the median elements throughout its length

*Amia.* (Fig. 6.)

In *Amia* the maxillo-palate is slung to the skull in precisely the same way as in the great majority of the bony fishes. The relative importance of the hyomandibular and ethmo-maxillary fixations is the same as in Teleostei.

No. 1 differs from No. 1 in *Polypterus* in that its ascending process is large, the palatine lamina is very small, and lateral line canal organs are absent. Like the bone in *Polypterus*, this is planted directly upon the cartilage and to a certain extent its ascending process replaces the anterior part of the ethmoid cartilage. The alveolar edge is set with teeth. The palatine process is very narrow and does not extend back to suture with the anterior end of No. 7a. The bone is sutured to No. 2 along its postero-lateral margin.

No. 2 is planted on the anterior end of the palato-quadrate cartilage, it presents a strong alveolar ridge, a narrow palatine plate and a more extensive ascending lamina. It is firmly sutured to No. 1 in front by the palatal lamina and alveolar ridge. It is also sutured to No. 5 along its median edge and to No. 6 along the posterior edge of the palatine lamina and the alveolar ridge. It is firmly bound to No. 5 above it. The anterior tip of the maxillary labial bone is wedged into a socket between the alveolar ridges of this bone and No. 1.

No. 1b. Each of these bones is an elongated lamina planted upon the ventral surface of the ethmoid cartilage, and extending forward to lie below the narrow palatine process of No. 1. Posteriorly they suture with the front end of No. 7a. Anteriorly they are fused together and are bound to No. 1a very firmly, but there is no true suture.

No. 4 is a thick plate of bone which is firmly sutured to Numbers 2, 5 and 6 and forms the outer part of the palate. The lateral edge of the bone is free between No. 2 and its extreme posterior end, where the bone makes a small contact with the quadrate.

No. 5 is a triangular plate with its median edge free, the lateral edge suturing with 2 in front and 4 behind, and the posterior edge sutured to No. 6.

No. 6 is an irregularly shaped flat bone which is firmly sutured to Numbers 4 and 5 and to the quadrate. There is an upward and medially-directed process of this bone which is firmly bound to the prootic region of the skull.

Bones 4, 5 and 6 are all carried on the palato-quadrate arch and appear on both dorsal and ventral views. Much of the cartilage remains in the adult and is seen in the dorsal view between the bones.

No. 7a is more extensive than in most other fishes, and has ascending processes, which cover the myodome antero-inferiorly, and an alisphenoid process which sutures with the alisphenoid bone.

No. 8 is a small ossification on the postero-lateral corner of the ethmoid cartilage; it does not present in the palate.

*Teleostei.* (Fig. 7.)

The maxillo-palate is hyostylic and movably jointed to the ectethmoid in front. In some forms, e.g., certain mormyrids, the palate is firmly attached along more or less of its length to the skull by the firm sutural union of 5 and/or 6 to 7a. This, however, is exceptional. The two halves of the palate are usually bound together by a palatine fascia which extends across the mid-line below, but bound to, 7a. In some forms the palatine fascia is attached to the lateral margin of 7a, which thus appears in the palate, at least anteriorly.

No. 1b + 3 is variable. It may or may not bear teeth. It is always planted on the front end of the ethmoid cartilage. It may be a flat bone confined to the ventrum of the cartilage, or it may have both palatine and ascending processes. Finally, and this is the



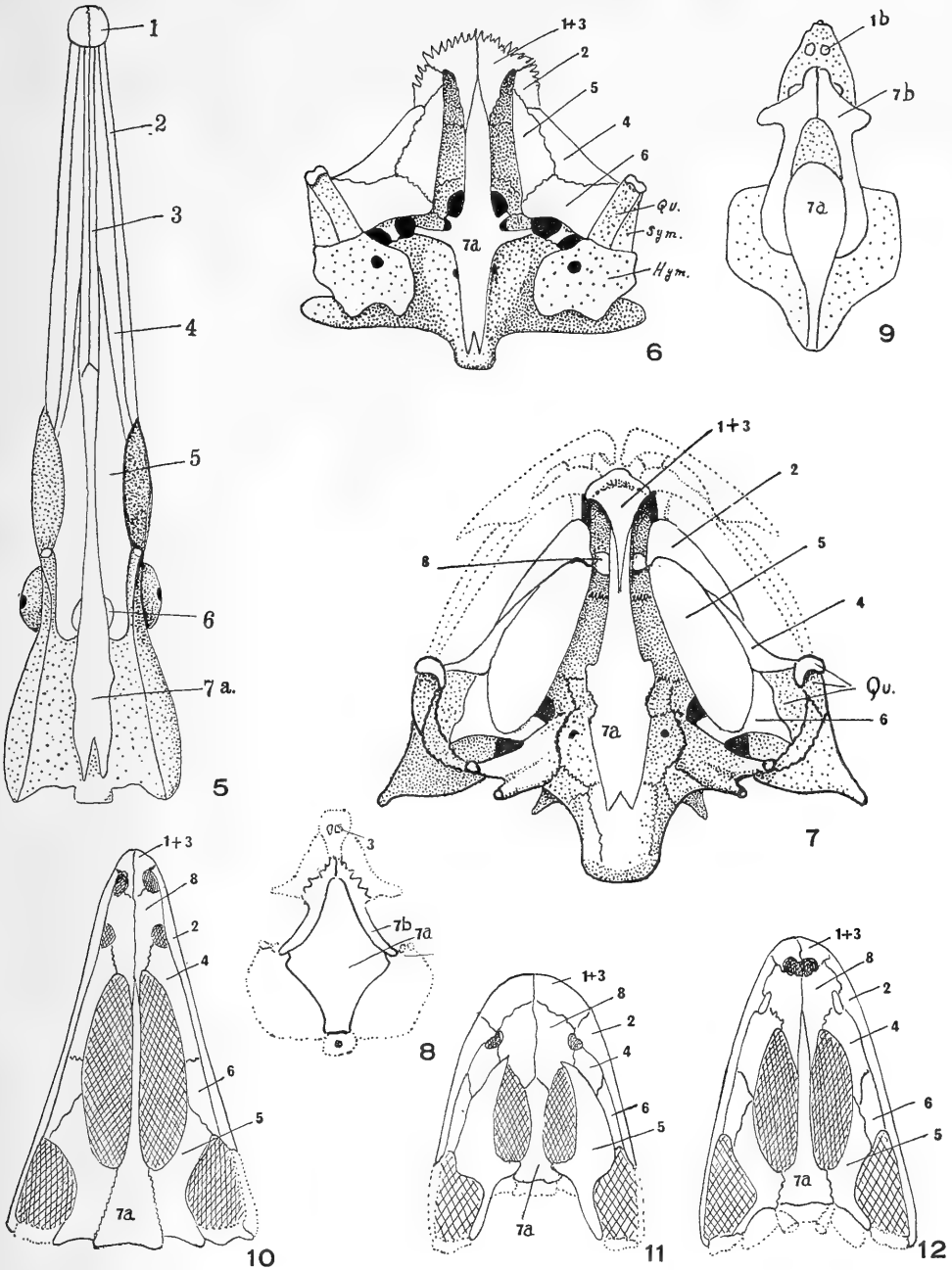


Fig. 5.—*Lepidosteus* (from Parker).  
 Fig. 6.—*Amia* (from Bridge).  
 Fig. 7.—*Epinephalus* (from Kesteven).  
 Fig. 8.—*Ceratodus* (from Kesteven).  
 Fig. 9.—*Lepidosiren* (from Bridge).  
 Fig. 10.—*Trematosaurus* (from Watson).  
 Fig. 11.—*Eryops* (from Watson).  
 Fig. 12.—*Capitosaurus* (from Watson).

commonest form, it is a solid-seeming mass of bone replacing, more or less completely, the anterior part of the cartilage. This form is, however, very seldom absolutely solid, and in the majority of instances, it is a hollow shell presenting smooth unbroken surfaces antero-superiorly, ventrally and laterally, but more or less open posteriorly where its edges suture with 7a ventrally, 8 laterally and with the mesethmoid and/or dermal scutes dorsally. Of these sutural contacts the constant ones are those with 7a and 8.

In some of the Teleostei the labial premaxillae and maxillae are not developed, e.g., *Apodes*; in these fishes the bone 1b + 3 functions as the premaxilla (Kesteven, 1926).

No. 2 is commonly a relatively solid bone, thick at its anterior end, where also it usually presents an ascending lamina. The dorsal surface of this thickened anterior end is always firmly attached to No. 8, with a joint cavity between the two bones, in all but very exceptional instances. The expanded palatine lamina is firmly sutured to the lateral margin of No. 5 and posteriorly it most commonly is sutured to the anterior end of No. 4.

No. 5 is the most extensive bone in the palate. It is a long flat bone which is firmly sutured to 2, 4 and 6 laterally. It may also be bound to the quadrate between 4 and 6. Except in these exceptional instances where the bone is sutured to 7a, its median margin carries the attachment of the palatine fascia.

No. 4 is commonly a curved splint attached along the lateral margins of Numbers 2 and 5. It may extend back far enough to suture with the quadrate.

No. 6 is one of the most variable bones in the palate. The only constant relations are sutural union with 5 and the quadrate.

Numbers 5 and 6 give origin to muscles of mastication and respiration and they are strengthened by low ridges and flanges on the dorsal surface.

No. 7a has lateral flanges posteriorly which rise on the lateral wall of the myodome, and reach and, in some fishes, cover, the side of the basioccipital and lower otic bones.

No. 8 is a more or less solid ossification of the postero-lateral corner of the ethmoid cartilage. It is sutured to 1b + 3 in front, to the mesethmoid dorso-medially, to the prefrontal dorso-laterally, and with the anterior end of 7a ventro-medially. Laterally to this last suture it carries the joint area for articulation with No. 2.

In a majority of the teleosts this bone presents in the palate medially to No. 2.

Attention is drawn to the fact that throughout the teleostomes this is the bone to which the maxillo-palate is attached anteriorly.

#### (B). AMPHIBIA.

##### 1. EUAMPHIBIA.

*Dipnoi.* (Figs. 8 and 9.)

The quadrate, entirely cartilaginous, is attached to the skull by ascending, basal and otic processes. There is no maxillary or palatal arch. Living dipnoans are peculiarly specialized. They have lost all the bones and cartilages of the maxillary and palatal arches, and so little is known about the fossil forms that they throw no light on the stages in this loss.

Bones 1, 2, 4, 5 and 6 are missing altogether.

No. 3 is a small plate of bone bearing teeth, placed on the ventrum of the ethmoid cartilage, an appreciable distance behind its anterior end.

No. 7a is an extensive plate of bone planted on the central area of the ventrum of the skull and extending backwards beyond it. It does not reach so far forward as the bone does in the fishes.

No. 7b is a flat curved splint also planted directly on the ventrum of the skull. Its posterior one-third lies below the processus basalis of the quadrate. In *Ceratodus* it sutures with the antero-lateral edge of 7a and meets its antimere in front of that bone in a median suture.

7a and 7b form the floor of the canal for the palatine branch of the facial nerve.

In *Lepidosiren* there is a gap between 7a and 7b, the latter extends directly forward and then bends inward abruptly to meet its fellow a short distance in front of 7a.

*Stegocephalia.* (Figs. 10, 11 and 12.)

The suspension is monimostylic. The actual mode of attachment of the quadrate to the skull is obscured by the bones investing it. There is, however, every reason to believe that ascending, basal and otic processes were present since they are present in every living amphibian. The well-developed maxillo-palate was strengthened by an antero-laterally directed arm of No. 5, which was firmly sutured to 7a on the ventrum of the basisphenoid and extended forward to be sutured to the palatal arch laterally in front of the orbit. A further strengthening of the maxillary arcade was effected by a quadrato-jugal bone. Anteriorly the palate was attached to the ventrum of the ethmoid region of the skull by the paired bones 8. These were sutured to 1, 2 and 4 laterally and to 7a medially, and were doubtless firmly attached to the ethmoid cartilage.

Numbers 1 + 3 and 2 present palatine laminae, alveolar margins and ascending dermal processes.

No. 8 is a plate of bone which is firmly sutured to Numbers 1 + 3, 2, 4 and 7a.

No. 4 may suture with No. 5 along its median border, but more commonly that bone does not reach far enough forward to meet it, in which case the median edge is free, and forms part of the lateral boundary of a subocular vacuity between No. 7a and the maxillary arch.

No. 6 is a small plate introduced between the posterior end of No. 2 and No. 5. It is not always present. In its absence No. 4 may intervene between 5 and 2 or in some forms No. 5 makes sutural union with 2.

No. 5 is a solid flat bone securely anchored to the base of the cranium and thereon suturing with 7a. This bone extends from the skull base, always behind and lateral to the subocular vacuity, forward and laterally to suture with Numbers 6, 4 and 2. In some forms (e.g., *Eryops*, Fig. 11) it is continued forward to meet No. 8. In such case it forms the entire outer boundary of the subocular vacuity. No. 5 has a postero-lateral ramus, whose size appears to have been decided by the distance of the articular head of the quadrate from the skull, for it extends along the ventrum of the body of the quadrate to just short of the articular head.

No. 7a, though an extensive bone, is not as large as in the fishes.

#### *Cocilians.* (Figs. 13 and 14.)

The maxillo-palate is attached to the skull as in the Stegocephalia.

Bone No. 6 is absent.

No. 5 is markedly reduced, all that remains of the bone seen in the stegocephalians being the anterior arm. The articular head of the quadrate is attached close to the base of the skull, and the posterior end of No. 5 is sutured to No. 7a and the quadrate. Anteriorly, 5 sutures with 4. As in the stegocephalians, there is a subocular vacuity between 5 and 7a.

No. 7a is a much broader bone than in the fossils. It sutures with No. 8 anteriorly and also has a very short suture with 4 just where the post-narial process of that bone sutures with No. 8.

The post-narial process of No. 8 is a constant feature of this bone, which differs from that of the fossils in that it extends forward lateral to the post-narial opening. In this situation it occupies the place of the palatine lamina of No. 2 in the fossils.

#### *Urodela.* (Figs. 15 and 16.)

The suspension of the maxillo-palate is similar to that in the other amphibians. The bony connection by No. 5 between the posterior end of the arcade and the base of the cranium is commonly broken and that between No. 2 and the quadrate is missing.

Numbers 1 + 3 and 2 are similar to those bones in the other two groups in that their ascending processes suture with components of the dermal roof.

No. 8 is essentially similar to the bone in the other forms.

No. 4 is reduced in size in most Urodeles, but lies on the ventrum of the ethmoid cartilage and still serves as the bone which connects No. 2 to the median pair 8.

No. 5 is a relatively more expanded bone than in the stegocephalians, but its anterior arm does not usually reach either No. 2 or No. 4. Its antero-medial border is the lateral boundary of the subocular vacuity.

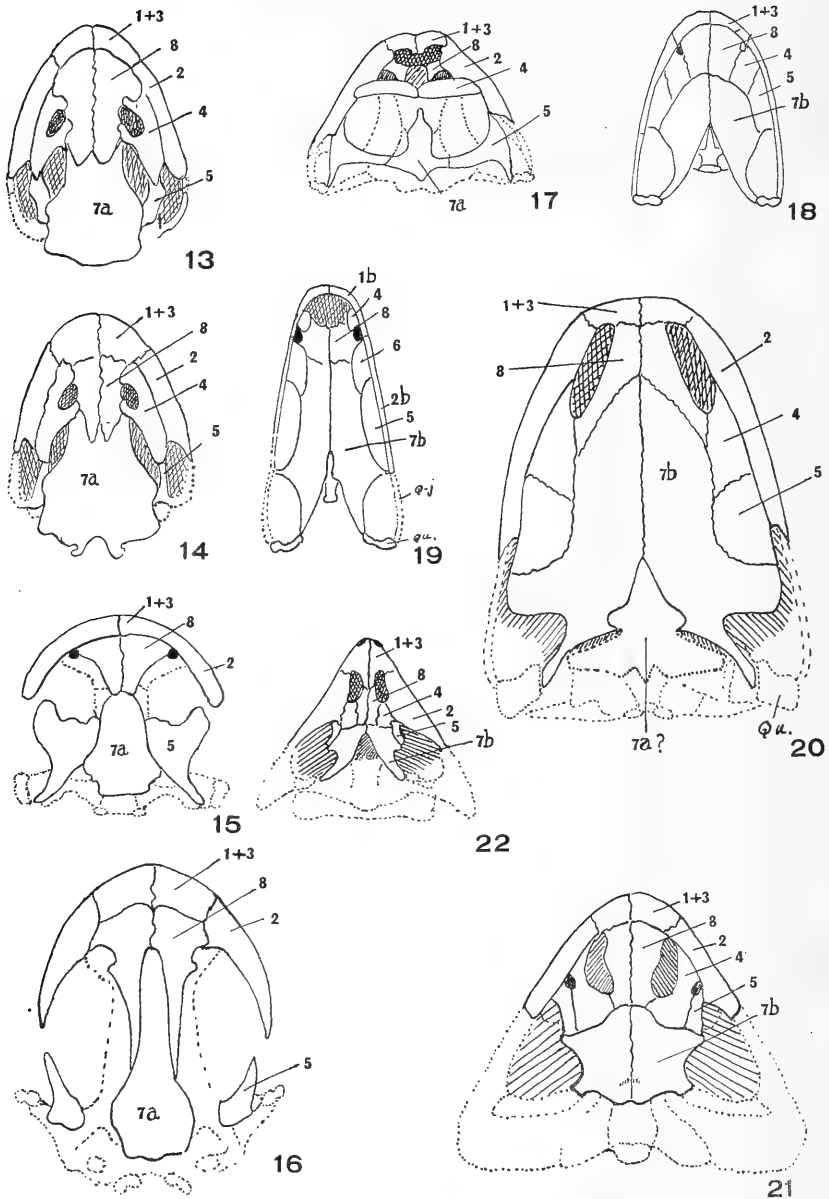


Fig. 13.—*Ichthyophis* (from Wiedersheim).  
 Fig. 14.—*Siphonops* (from Wiedersheim).  
 Fig. 15.—*Sieboldia* (from Parker).  
 Fig. 16.—*Triton* (from Parker).  
 Fig. 17.—*Bufo* (from Parker).  
 Fig. 18.—*Baphetes* (from Watson).  
 Fig. 19.—*Orthosaurus* (from Watson).  
 Fig. 20.—*Seymouria* (from White).  
 Fig. 21.—*Parciasaurus* (from Broom).  
 Fig. 22.—*Procolophon* (from Broom).

No. 6 is missing.

No. 7a is similar to the bone in the stegocephalians.

*Anura*. (Fig. 17.)

The illustration of the maxillo-palate of *Bufo* is given rather than omit the group altogether. It is not felt that any description of so well-known a type is necessary.

#### SAURAMPHIBIA.

*Baphetes* (Fig. 18) and *Orthosaurus* (Fig. 19).

The whole maxillo-palate was rigidly attached to the skull. The manner of attachment of the quadrate to the skull is not clear. Watson (1926) identified an "epipterygoid", but he does not state whether this is to be regarded as the homologue of the cynodont "epipterygoid" or whether it is the ascending process of the quadrate.

The most striking feature of the maxillo-palate of the Embolomeri is the extreme reduction, and it may be absence, of No. 7a and its replacement by the two large 7b bones. The result is so close a resemblance to the primitive type of saurian palate that there is little doubt these amphibians belong to the ancestral stock from which the Sauria were evolved.

Bones 1 and 2 are of the amphibian type, that is, narrow, tooth-bearing bones practically devoid of palatine laminae.

The size and position of bones 8, 5 and 6 are essentially as in the stegocephalians, but also essentially as in the cotylosaurs.

7b is a very extensive bone and, as in primitive reptiles, it meets its antimere in a median suture.

#### (C). SAURIA.

##### 1. REPTILIA.

*Cotylosauria*. (Figs. 20, 21 and 22.)

In *Seymouria* (Fig. 20), according to White (1939), the bone 7a is present fused to the basisphenoid.

7b is a very extensive bone which, as in all but specialized reptiles, meets its fellow in a median suture. In *Parciasaurus* (Fig. 21) No. 7a has been described, 7b is much less extensive. Numbers 4 and 5 suture with the lateral edge of 7b in *Seymouria*. These two bones suture with the front margin of the smaller 7b in *Parciasaurus*. Bone 8 is relatively more extensive in *Parciasaurus*.

In *Procolophon* (Fig. 22) No. 7a has been described and 7b is still further reduced. Numbers 1 + 3 and 2 have both extensive palatine laminae and 4, 5 and 8 are correspondingly reduced.

The development of palatine laminae of bones 1 and 2 in so primitive a reptile as *Procolophon* is particularly interesting, because the continued increase in those laminae leads to that reduction of other bones of the palate seen in process in the cynodonts and completed in the Theria.

*Chelonia*. (Figs. 23, 24 and 25.)

Numbers 1 + 3 and 2 are essentially similar bones. Each presents a strong alveolar ridge and palatine and ascending processes. The palatine process is variable in extent but is always well developed. These processes are firmly sutured to No. 8, but posteriorly No. 4 lies between 8 and the palatine process of 2.

No. 8 is always very strongly developed. It lies between the pair of bones No. 4 and commonly extends forward to suture with both 1 + 3 and No. 2. Posteriorly it sutures with No. 7b. The bone lies between the two post-narial passages and sutures with both frontal and prefrontal bones dorsally. It may present two palatine surfaces, one anterior to the choanae, the other posterior thereto. This bone is the "cornerstone" which binds the maxillo-palatal arch together and anchors it to the skull medially. In some forms the bone is largely covered ventrally by the palatine processes of No. 2 and by No. 4.

No. 4 is a thick plate of bone which connects No. 2 to No. 8 and supplies an extensive area of the palate between these bones. Exceptionally No. 4 meets its

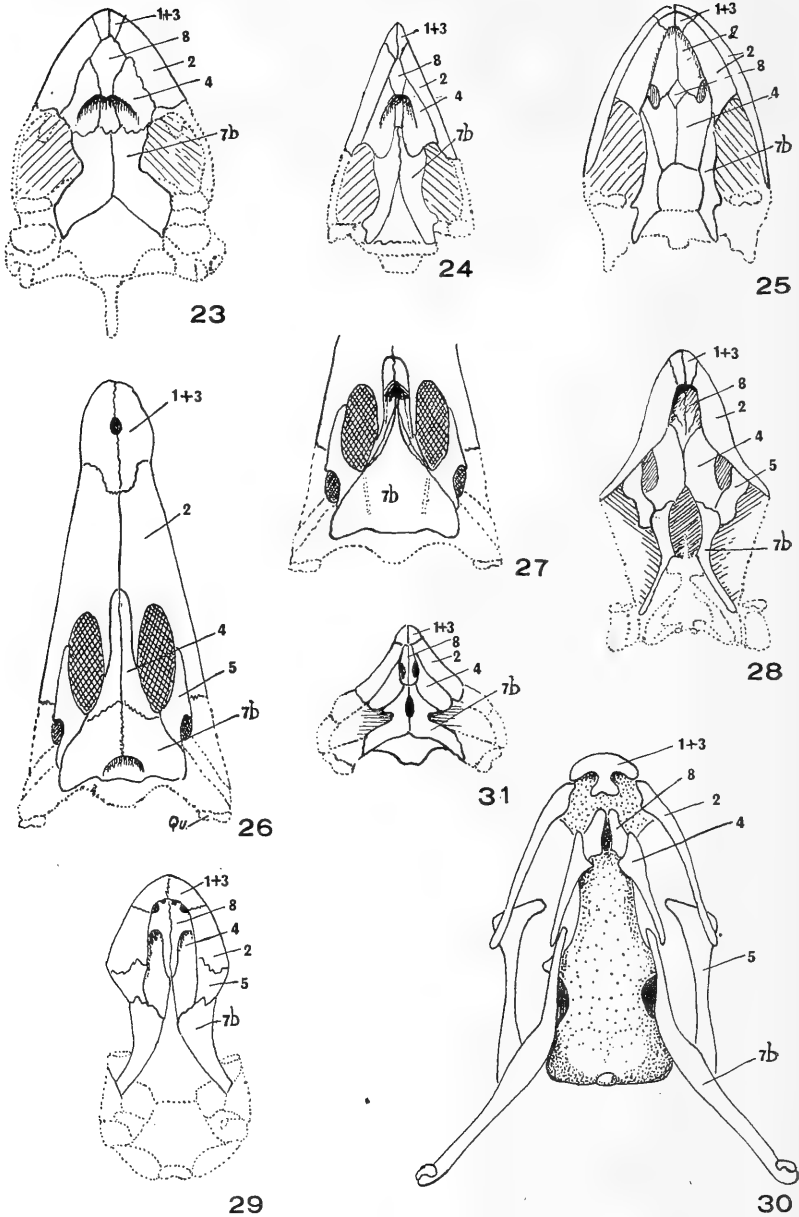


Fig. 23.—*Chelone* (from Kesteven).  
 Fig. 24.—*Chelone* (from Kesteven).  
 Fig. 25.—*Carettochelys* (from Kesteven).  
 Fig. 26.—*Crocodilus* (from Kesteven).  
 Fig. 27.—*Crocodilus* (from Kesteven).  
 Fig. 28.—*Tiliqua* (from Kesteven).  
 Fig. 29.—*Amphisbena* (from Williston).  
 Fig. 30.—The Snake (from Parker and Bettany).  
 Fig. 31.—*Hyperodapedon* (from Williston).

antimere in a median suture, in which case it covers the posterior part of No. 8. Typically No. 4 provides part of the floor of the post-nasal passage, most of the side wall and part of the roof as well.

Numbers 5 and 6 are missing.

No. 7*b*. In *Chelone midas* the two bones occupy the situation of 7*a* in the Euamphibia. Each is a relatively thick flat bone sutured directly to the ventrum of the basisphenoid bone, and extending forward along the base of the skull below the orbit to suture with Numbers 4 and 8, and in some other species, with the palatine process of No. 2. Dorsally these bones may suture also with the antero-medial corner of the prootic bone. On either side of the rostrum basisphenoidei they commonly develop an alisphenoid lamina which sutures with a downwardly-projecting alisphenoid lamina of the parietal, and with the epipterygoid bone. The postero-lateral portion of the bone lies below and sutures with the body and basal process of the quadrate. Typically the two bones meet in a median suture for the greater part of their length but in some forms, e.g., *Carretochelys* (Fig. 25) they are separated by nearly the full width of the basisphenoid and have the pair of bones No. 4 between them anteriorly, but there is never any suborbital or other vacuity between them and the skull base.

The relation of the nervous palatine facials to this bone will be found to be important in later discussion. The nerve lies in a canal, the parabasal canal, which commences in and runs through the substances of the basisphenoid bone in its posterior portion, and then comes to lie between the ventrum of that bone and the dorsal surface of No. 7*b*.

*Crocodylia*. (Figs. 25 and 26.)

Numbers 1 + 3 and 2 have ascending, alveolar and palatine processes, the last being particularly extensive. The whole snout is, of course, much elongated and No. 2 has made the largest contribution to the increased length of the maxillo-palate.

No. 4 is a narrow bone which sutures with its fellow in a median suture, with the palatine lamina of No. 2 laterally and with the palatine lamina of No. 7*b* along the posterior margin. Dorsally this pair of bones makes sutural contacts which do not appear in the palatal view. Anteriorly they suture with the prevomer and posteriorly, along the median palatine suture, they are sutured to the vomerine plate of No. 7*b*.

No. 5 is sutured to No. 7*b* just behind the transpalatine suture, this part of the bone being continued backward and slightly dorsally to suture with the quadrate. From the suture with No. 7*b* the bone passes forward and laterally to suture with the posterior end of No. 2. A suborbital vacuity is present between the lateral edge of the palatine and No. 5. This vacuity extends forward in a bay in the posterior end of the palatine lamina of No. 2.

No. 7*b* is a particularly interesting bone. In the adult there is no suture between the two halves of the bone. There are three very definite parts to this bone, the body, naso-palatine and naso-vomerine processes. The body is triangular in outline, being placed directly upon the anterior portion of the ventrum of the basioccipital and the whole of the ventrum of the basisphenoid. The lateral parts of the body rise abruptly on the sides of the basal bones and each sutures with that part of the quadrate which lies below the otocrone. From this body there stands down on each side a nearly vertical ridge which curves medially and, entering the horizontal plane, reaches that from the other side in a median suture. Anteriorly the horizontal laminae suture with the posterior edges of bones No. 4. The naso-vomerine process commences as a ridge, and continuing forward extends further ventrally to provide a complete inter-narial septum for the posterior part of those passages. This process sutures with the median palatine suture and its anterior edge, which is double (the process is shaped like the letter V), sutures with the posterior margin of No. 8 along a line which, commencing behind at the ventral edge of the interorbital septum, falls to the dorsal surface of the suture between the two No. 4 bones. The trough of the V-shaped portion is filled by the base of the interorbital septum. It is stressed that there is no trace of a suture between the two halves of the body or the naso-vomerine process.

No. 8 does not appear in the palate at all, but it is none the less an important component of the maxillo-palate. It has been covered ventrally by that expansion of the palatine laminae which has closed and thrown the choanae so far back. It forms the inter-narial septum anterior to the naso-vomerine process of No. 7b and extends from the roofing bones of the passage to the saggital suture along the dorsal surfaces of No. 4 and the palatine laminae of No. 2.

*Lacertilia.* (Figs. 28 and 29.)

The typical lacertilian maxillo-palate such as that of *Lacerta* or *Tiliqua* (Fig. 28) is so well known that its adult form calls for little description. Attention is drawn to the fact that there is no subocular vacuity medial to No. 7b and that this bone is attached to Numbers 4 and 5 anteriorly, to the quadrate behind, and to the basisphenoid by a process which is characteristic of the lacertilians and a few other reptiles.

No. 8 is reduced in size and is no longer the structurally important feature it is in chelonian palates. It is a small squame supporting part only of the nasal organ and hardly contributing to either palatal structure or stability.

No. 4 has, in these palates, assumed the duty of supporting and holding together the arch which is performed by No. 8 in chelonians. These two bones are relatively solid and they are firmly united together and to Numbers 2, 5 and 7b in the palate and to descending processes of the frontal bones dorsally.

The maxillo-palate of *Amphisbena* (Fig. 29) differs from the typical lacertilian form in several important respects. The most striking of these is that No. 7b is a broad bone which has all the relations of the same bone in the chelonians, except that it sutures in front, laterally to the suture with No. 4, with No. 5, a bone not present in the chelonian palate; also there is no suture with No. 8.

No. 8 is larger than in the typical lacertilian condition and does serve to some extent in strengthening the maxillo-palatal arch, though not to the extent seen in the chelonians. There is no gap between No. 7b and the base of the skull as in the lacertilians generally and there is no basipterygoid process.

*Ophidia.* (Fig. 30.)

The maxillo-palate of the ophidians is essentially a specialized modification of that of the lacertilians, and the embryology of the component bones is essentially the same. It is not thought that this maxillo-palate throws any light upon the evolution of the therian palate not thrown by the lacertilian condition. No description is offered and the palate has been illustrated only to make the series complete.

*Rynchocephalia.* (Fig. 31.)

*Sphenodon* resembles the Lacertilia in the separation of the two 7b bones and in the presence of a basipterygoid process. In *Hyperodapedon* (Fig. 31) the primitive condition is present, these bones meet in a mid-line suture and there is no basipterygoid process.

2. AVES.

*Emeus.* (Fig. 32.)

Bone 7a is not present. 7b is reduced to a small bone placed medially to the processus ascendens quadrati, and articulating with the basis-cranii either through a basipterygoid process of the basisphenoid as in *Emeus* or through a process on the presphenoid. In both forms a joint cavity is present at the point of articulation. Numbers 1 + 3 and 2 commonly have very extensive palatine processes. No. 8 is relatively extensive but is usually not a strong bone. No. 4 is always well developed, but Numbers 5 and 6 are never developed.

MISCELLANEOUS FOSSIL REPTILES. (Figs. 34, 35, 36, 37 and 38.)

These have been included because they illustrate variation in the size and position of the component bones. There is general agreement that the bones similarly numbered are homologous. These maxillo-palates will not be described, but the drawings are reproduced because they provide factual evidence of extreme ranges of variation in the



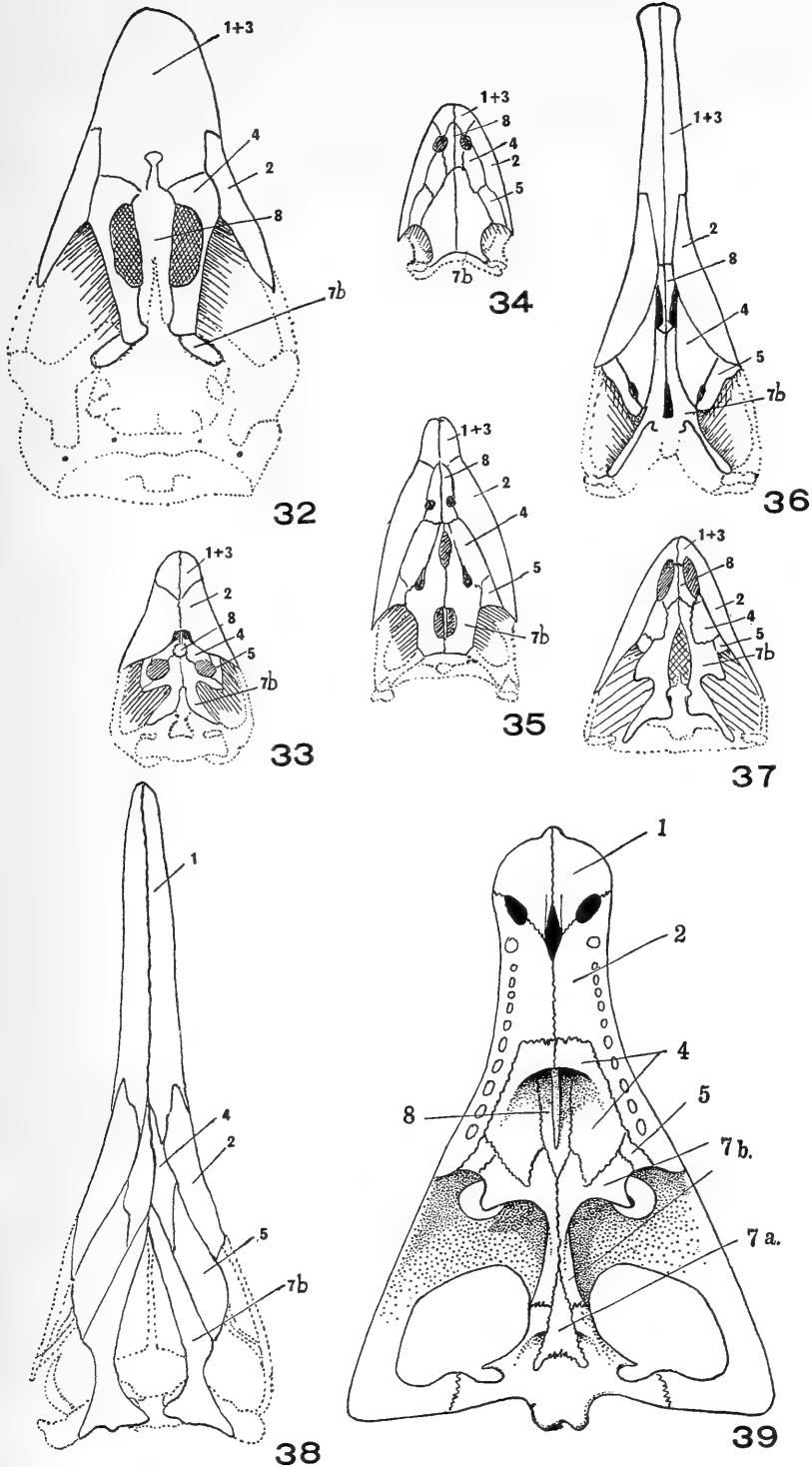


Fig. 32.—*Emeus* (from T. J. Parker).  
 Fig. 33.—*Bauria* (from Broom).  
 Fig. 34.—*Simosaurus* (from Williston).  
 Fig. 35.—*Thaumatosauros* (from Williston).

bones—evidence that the maxillo-palate as a whole and in its parts has been exceedingly plastic.

*Theriodontia.* (Figs. 38 and 39.)

The most striking feature of the theriodont palate is probably the increase in size of the palatine laminae of 1 and 2 and the corresponding reduction in 4 and the even greater reduction in 5, and complete loss of No. 6.

Numbers 1 and 2 do not need description.

No. 4 in *Bauria* lies entirely behind and above the choanae, and the nasal passages

No. 4 in *Bauria* (Fig. 33) lies entirely behind and above the choanae, and the nasal passages are floored by the palatine laminae of 1 and 2. No. 4 sutures with No. 8 and with 7*b*, all three of these bones being in contact with median elements of the skull dorsally where these sutural contacts are made.

No. 8 resembles that bone in the chelonians in that it sutures with Numbers 4 and 7*b* above and behind the choanae and with the palatine lamina of 2 on the floor of the post-nasal passage. It also resembles the bone in the chelonians in its relation to median skull elements dorsally, and in serving as the median support of the palate.

No. 7*b* is of the primitive type.

No. 5 is a small bone which extends between a lateral process of 7*b* and the posterior margin of the palatine process of 2. Medial to the suture with the last bone, 5 sutures with the postero-lateral corner of 4.

*Cynognathus.* (Fig. 39.)

The anterior portion of this maxillo-palate resembles very closely the chelonian on the one hand and the mammalian on the other.

Bones 1 and 2 both have extensive palatine laminae.

No. 4 has a narrow palatine lamina, which forms the floor of the post-nasal passage posteriorly and sutures with No. 2 and an ascending lamina, which forms the side wall of the post-nasal passage and curves medially to form the roof of the passage and a large part of the palate posteriorly to the choane, and in this part sutures with 8, 5 and 7*b*.

No. 8 supplies a narrow area of the roof of the post-nasal passage on either side of the mid-line and has a strong vertical lamina which divides the two passages and sutures with the median suture between the two No. 4 bones.

No. 5 is a much reduced bone placed between the antero-lateral corner of 7*b* and the postero-medial edge of No. 2.

No. 7*b* shows a very interesting reduction posteriorly. Behind the palatal laminae the bone is reduced to a narrow splint, apparently applied to the base of the presphenoid bone.

No. 7*a* is reduced to a small triangular area on the base of the skull.

(D). THERIA.

(Figs. 40, 41, 42 and 43.)

The maxillo-palates of both the monotremes are very certainly peculiarly specialized, but inasmuch as that they are derivable from the less specialized saurian palate, they have been illustrated; one marsupial and one mammalian maxillo-palate are also illustrated, but none of these calls for detailed description.

The outstanding feature of the maxillo-palate of the Theria, when compared with that of the Sauria, is the culmination of certain tendencies which can be recognized in the latter.

Firstly, the whole structure has moved forward relative to the brain case and there has been a gradual reduction almost to extinction of the important 7*b* which contributes so largely to the posterior portion of the maxillo-palate. All that remains of the bone is

Fig. 36.—*Machaeroprotopus* (from Williston).

Fig. 37.—*Pariotrichus* (from Broom).

Fig. 38.—*Ichthyosaurus* (from Sollas).

Fig. 39.—*Cynognathus* (from Parrington and Westoll, modified).

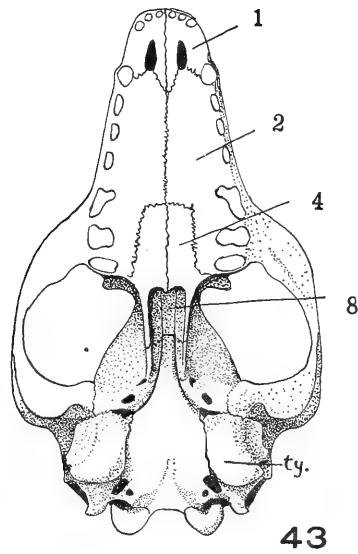
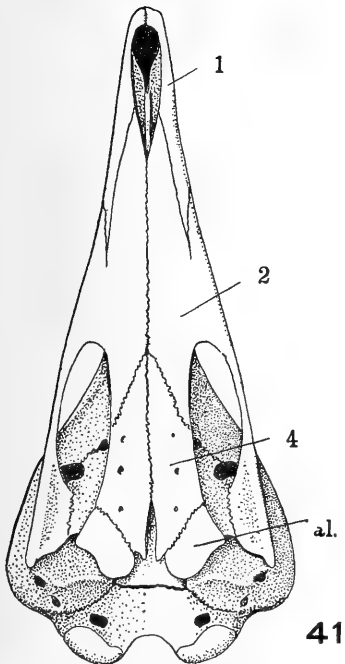
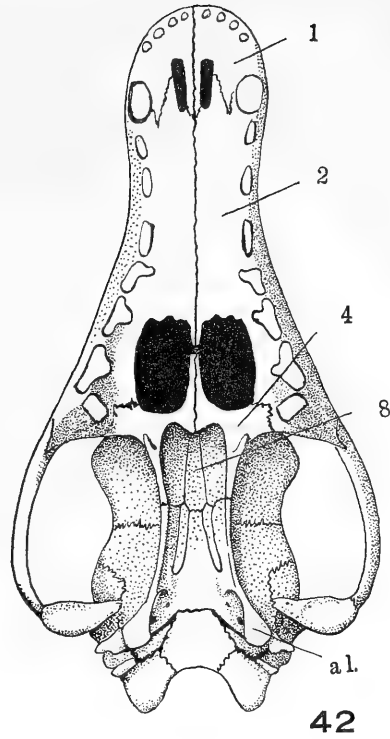
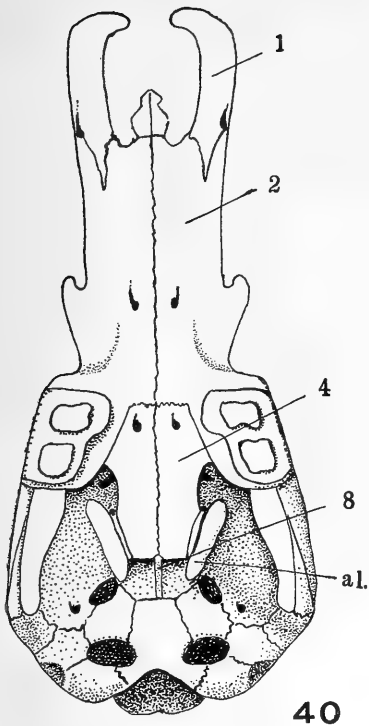


Fig. 40.—*Ornithorhynchus* (from Kesteven and Furst). al., tympanic wing of alisphenoid.

Fig. 41.—*Echidna*. al., see Fig. 40.

Fig. 42.—*Thylacinus*. al., see Fig. 40.

Fig. 43.—*Canis*. ty., tympanic bulla.

a small flange which projects ventrally from the sphenoid region of the skull on either side of the posterior end of No. 8.

No. 5, so important a structural unit in the Amphibia, and serving the same function in most saurians, but reduced almost to extinction in the Theriodontia, is no longer recognizable but may be present, as suggested by Parrington and Westoll (1940), as the ventral moiety of No. 7*b* in those forms in which the bone ossifies from two centres.

No. 6 has gone entirely.

No. 4, though reduced in size, is still an important bone. As in some chelonians and cynodonts, it has developed ascending laminae which not only provide part of the lateral wall of the post-narial passage, but, being anchored to the skull above, serve, together with No. 8, to strengthen the palate.

No. 8 is always well developed and still serves as the central support of the palate.

Numbers 1 and 2 have each developed extensive palatine laminae and these four constitute practically the whole of the actual palate.

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THE ANATOMY OF TWO NEW DIGENETIC TREMATODES FROM TASMANIAN  
FOOD FISHES.

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(Communicated by Dr. S. W. Carey.)

(Eight Text-figures.)

[Read 29th May, 1946.]

INTRODUCTION.

In May, 1945, three specimens of the "Colonial Salmon" (*Arripis trutta* Bloch and Schn.) of the southern waters of Australia were examined for intestinal parasites. One specimen was quite free from infection but the intestines of the remaining two specimens appeared brown in colour due to the eggs within the bodies of innumerable small trematodes. The majority of the worms were under 1 mm. in length and apparently belonged to the Monorchiiidae.

About one in every fifty worms, however, was a larger form representing a new species of the Bucephalidae. As this species does not fit into any known genus it is proposed to erect a new genus *Telorhynchus* to receive it. The present paper gives a definition of the new genus and an account of the trematode on which the genus has been established. In addition, a new species of *Helicometra* (Allocreadiidae) from the gut of the "Rough Gurnet Perch" (*Neosebastes thetidis* Waite) is described.

Whole mounts were fixed in alcohol under slight cover-glass pressure, and stained with alum-carmin. Specimens intended for sectioning were fixed with Bouin's solution. Sections were stained with Ehrlich's haematoxylin and eosin.

Genus TELORHYNCHUS, n. gen.

*Diagnosis:* Prosorhynchinae of elongate form. Rhynchus tapered internally and armed with a single circllet of spines, interrupted in the mid-ventral line. Body covered with minute spines. Testes directly, or slightly obliquely, one behind the other in posterior half of body. Ovary pretesticular. Vitellaria in a convex bow in the fore-body. Uterus not extending anterior to the vitellaria. Laurer's canal present. True seminal vesicle absent. Mouth situated near middle of the body-length. Intestine simple, saccular, directed forwards from the mouth.

TELORHYNCHUS ARRIPIDIS, n. sp.

*External Features:* The worms are slender, elongate, and somewhat flattened dorso-ventrally. The dimensions of fifteen "in toto" mounts are 1.55-2.36 mm. long and 0.26-0.42 mm. broad, but living specimens are narrower and one and a half times as long as fixed specimens. The body is broadest at its middle length and tapers towards the extremities. It is narrowest immediately behind the crown of the rhynchus. The latter is hemispherical and bears two papillae anteriorly (Fig. 2). (These papillae do not represent contracted tentacles as is the case in some members of the Bucephalidae, as they are seen only when the animal is extended and are not noticeable in fixed specimens.) The rhynchus is notable in that it is armed with a single circllet of spindle-shaped spines, which are eighteen in number and measure 0.44 mm. long and 0.012 mm. in diameter. The circllet is interrupted in the mid-ventral line (Figs. 1-2). The body is covered by a thick cuticle with minute spinules 0.012 mm. long, closely arranged in transverse rows. The rhynchus is free from these spinules except within the ventral break in the circllet of spines. The mouth is situated on the ventral surface, at about

\* This work was carried out during the tenure of a Commonwealth Research Grant.

the middle length of the body when contracted, but at the junction of the second and last thirds of the body when extended. The genital aperture is in the mid-ventral line a short distance in front of the posterior extremity. The excretory pore is a median transverse slit at the posterior end of the body.

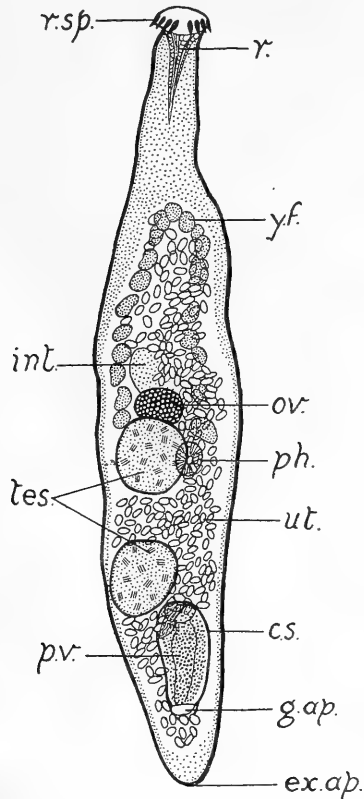


Fig. 1.—*Telorhynchus arripidis*, n. sp. Whole animal from the ventral aspect.

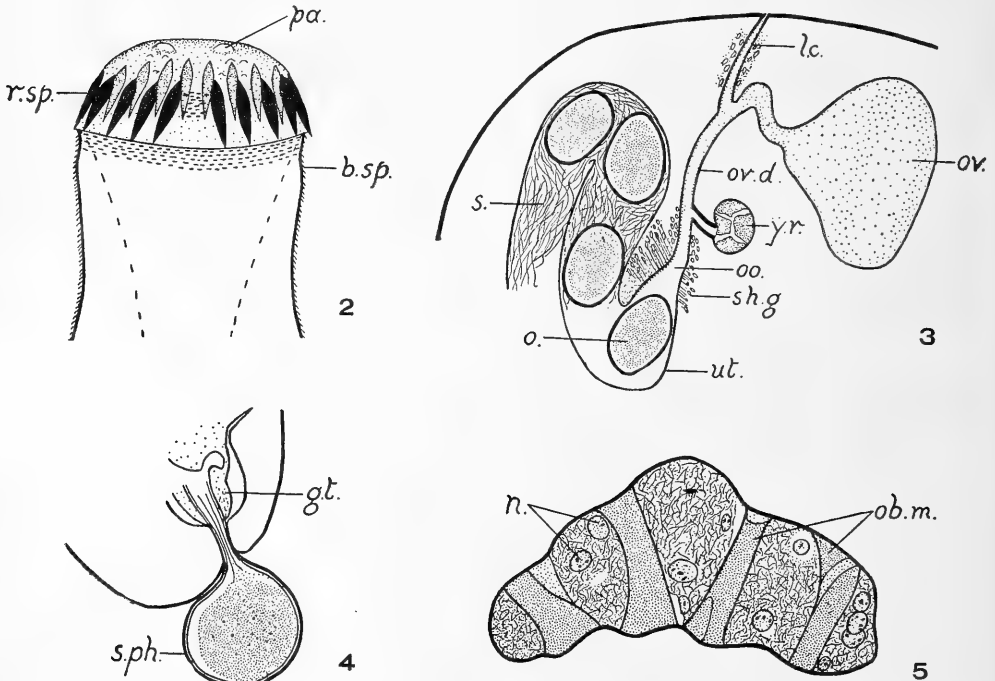
Abbreviations used in text-figures: ac., acetabulum; b.sp., body spines; c., cirrus; c.s., cirrus-sac; ex., excretory vesicle; ex.ap., excretory aperture; g.ap., genital aperture; g.t., genital tongue; int., intestine; i.s.v., internal seminal vesicle; l.c., Laurer's canal; met., metaterm; n., nuclei; o., egg; ob.m., muscles of rhynchus; oes., oesophagus; oo., ootype; o.s., oral sucker; ov., ovary; ov.d., oviduct; pa., papilla; p.a.p., preacetabular pit; p.g., prostate gland; ph., pharynx; p.p., pars prostatica; p.v., prostate vesicle; r., rhynchus; r.sp., rhynchal spines; r.s., receptaculum seminis; s., seminal fluid; sh.g., shell gland; s.ph., spermatophore; tes., testes; ut., uterus; y.f., yolk follicles; y.r., yolk reservoir.

**Digestive System:** There is no oral sucker, the mouth opening directly into the muscular pharynx. The pharynx is directed dorso-ventrally, and measures 0.06 mm. in length and 0.05 mm. in diameter. The inner circular muscles of the pharynx are very strongly developed but the radial muscles are very weak. The pharynx is generally displaced to the left of the mid-line by the anterior testis. Its position varies from immediately in front of the anterior testis to the level of the middle of that organ. The pharynx is surrounded by numerous large gland cells which are arranged laterally, closely appressed to the ventral body wall. The intestine is a simple elongate sac extending directly forwards from the pharynx a distance of approximately 0.33 mm., in about the mid-line. Its proximal end is narrow and may be termed an oesophagus. This region is surrounded by densely-staining cells which open into it and which, like those surrounding the mouth, probably secrete a digestive fluid. The wall of the intestine contains thin outer longitudinal and inner circular muscles, and, with the

exception of the oesophagus, is lined by an epithelium of tall cells which contain basal nuclei and distal vacuoles.

*Excretory System:* The excretory pore leads into a simple sac-like excretory vesicle. This extends forwards along the ventral side of the cirrus-sac and passes the pharynx on the right side. It may then expand somewhat before terminating at about the middle of the length of the intestine. The wall of the vesicle is very thin and extensible. Spherical droplets, due to an excretory product, are often present in the vesicle.

*Genital System—Male:* The testes are two entire, ovoid bodies lying directly or slightly obliquely in tandem within the posterior half of the body. They are always separated from one another as well as displaced on the right side, by the uterus, the anterior testis being usually nearer the right border of the body than is the posterior testis. The testes are approximately equal in size, the anterior one being occasionally larger than the posterior. Under slight cover-glass pressure they measure  $0.163 \times 0.163$ – $0.21 \times 0.24$  mm. and  $0.15 \times 0.18$ – $0.18 \times 0.24$  respectively. The vasa deferentia arise from the anterior borders of the testes. They immediately turn and run backwards along the left side of the testes to the base of the cirrus-sac. As the testes are arranged in tandem the vasa deferentia are very unequal in length. They enter the base of the cirrus-sac and expand into a large tubular seminal vesicle. No external portion of the seminal vesicle is present. The cirrus-sac is approximately cylindrical, measuring about 0.3 mm. in length and 0.1 mm. in diameter. It lies longitudinally or slightly obliquely in the mid-line immediately behind the posterior testis, its anterior end being often displaced to the left side and slightly in front of the posterior border of that organ. The cirrus-sac possesses a very thick muscular wall almost 0.01 mm. in thickness, composed of an inner layer of thin circular fibres and an outer layer of very stout longitudinal fibres. Towards the ends of the sac, the muscular wall is somewhat thinner. The seminal vesicle extends directly backwards for a distance not more than half the length of the cirrus-sac and usually considerably less. It then turns upon itself and passes into the pars prostatica



Figs. 2-5.—*Telorhynchus arripidis*, n. sp. 2. Ventral view of the rhynchus of an extended specimen, highly magnified. 3. Diagram of female complex, drawn from transverse sections. 4. Spermatophore projecting from genital pore. 5. Transverse section through the internal tapered portion of the rhynchus.



through a very narrow aperture surrounded by a sphincter. The pars prostatica forms a single anterior loop lying beside or ventral to the seminal vesicle. Its wall is membranous and is lined by an epithelium of relatively large thin-walled cells, which appear empty and almost fill the cavity of the pars prostatica, leaving only a narrow lumen. The posterior limb of the pars prostatica expands into a large prostate vesicle occupying most of the posterior half of the cirrus-sac. The wall of the vesicle is somewhat thicker than that of the pars prostatica and the epithelial lining of the latter is continued only as a narrow strip along one side of the vesicle. In the specimens sectioned the prostate vesicle was filled with fluid. The remaining space within the cirrus-sac is occupied by the prostate gland, which consists of a matrix containing numerous nuclei. Individual cells of the gland cannot be distinguished. A little in front of the posterior end of the cirrus-sac the pars prostatica passes into a short narrow ejaculatory duct. This leads into the genital atrium through a projecting genital tongue. The latter is a ventrally-directed prolongation of the posterior end of the cirrus-sac. It seems probable that the genital tongue functions as a copulatory organ. The genital sinus completely encloses the genital tongue and extends a short distance posterior to it before communicating with the genital pore. The sinus measures approximately 0.06 mm. in diameter. Numerous small gland cells are arranged radially about the genital sinus near the genital tongue. A large number of specimens taken from one of the fishes bore a single spherical spermatophore attached by a tapering stalk, which passed within the genital pore into the sinus. The spermatophore measures approximately 0.07 mm. in diameter when slightly flattened, and has a yellowish wall apparently chitinous in nature. A similar structure has been described as occurring in other species. As Ohdner (1905) points out, the gland cells surrounding the genital sinus closely resemble the shell gland cells of the female reproductive system. It appears certain that the spermatophores are produced within the genital sinus in the same manner as the eggs are formed within the ootype. The presence of the spermatophores throws doubt upon the suggestion that the genital tongue functions as a copulatory organ. Ohdner regards it as a rudimentary copulatory structure which probably assists in the formation of the spermatophores.

*Genital System—Female:* The ovary is a smooth spherical or ovoid body, which measures approximately 0.12 mm. in diameter. In some specimens it lies directly in front of the anterior testis, but in others obliquely to the left side of that organ. The ovary is never more posterior in position than the middle of the anterior testis and always lies towards the dorsal surface. Directly or obliquely backwards the ovary tapers into the oviduct. The largest ova are found in this tapered region. They measure as much as 0.01 mm. in diameter. The oviduct measures 0.008 mm. in diameter. It possesses a thin ciliated wall. A short distance from the ovary, Laurer's canal connects the oviduct with a pore on the dorsal surface to the left of the mid-line. Laurer's canal measures 0.006 mm. in diameter and only 0.04 mm. in length. It is surrounded by a glandular region containing numerous nuclei. The oviduct turns towards the ventral surface, narrows, and receives the central yolk duct from the yolk reservoir. The female duct proceeds a further short distance and expands into the ootype. This receives the fine ducts of the numerous surrounding cells which constitute the shell gland. The uterus retains the diameter of the ootype and continues as a convoluted tube towards the posterior end of the body. The proximal loops of the uterus contain darkly-staining masses of spermatozoa and therefore function as a receptaculum seminis. At about the level of the anterior end of the cirrus-sac the uterus turns and passes forwards on the left side of the body. It fills the body within the arc formed by the vitellaria, but does not extend into the neck region beyond. The uterus, still lying towards the left side of the body, then returns to the anterior end of the cirrus-sac. It crosses the body in front of the cirrus-sac and then passes backwards along the right side of that organ. After forming a single loop behind the genital sinus, the uterus opens into the sinus through a short and very narrow metraterm, the female aperture being ventral to the male opening. The eggs are dark brown in colour. They are ovoid, measuring  $0.04 \times 0.023$  mm. A large number of eggs are present in mature specimens, often to a great extent obscuring the internal organs.

The vitelline glands are irregular ovoid bodies arranged in a single series in the form of an inverted U within the anterior half of the body. The extremities of the arc extend backwards beyond the ovary on either side to about the level of the front border or the anterior testis. The vitellaria vary in number from 17 to 22, often appearing fewer due to their close appression to one another and to overlapping. The yolk cells are connected by two main ducts which run across from the free ends of the arc to a small reservoir situated behind the ovary. A short narrow central yolk duct, 0.012 mm. long, connects the reservoir with the female duct.

*Muscular System:* The body is peculiar in that it is divisible into cortical and medullary regions. The internal organs lie in a central spongy region, the spaces between the organs being traversed by attenuated membranous strands. The body-wall musculature is continuous with a dense glandular cortical region, which fills the entire body anterior to the vitellaria. The body wall contains the usual three layers, circular, longitudinal, and then oblique fibres. The fore-body is traversed by scattered, weak, dorso-ventral fibres. The external hemispherical portion of the rhynchus, bearing the single circlet of spines, is highly muscular having densely packed radial fibres. The long tapered internal portion of the rhynchus possesses a thin muscular wall, and contains four principal internal tracts of dorso-ventral fibres. The muscular tracts are arranged in a characteristic oblique fashion, there being two on either side of the sagittal plane (Fig. 5). Between the dorso-ventral muscle layers the rhynchus is filled with large gland cells.

*Nervous System:* A central nervous mass, consisting of two ganglia connected by a short thick commissure, lies immediately dorsal to the rhynchus and near its posterior end. Anteriorly, the ganglia are continuous with two stout nerves, which run forwards on either side of the rhynchus for a short distance before breaking up into fine nerves. Posteriorly the ganglia are continuous with two stout nerves which diverge and pass downwards to the ventral surface, in which position they continue backwards.

*Host:* *Arripis trutta* Bloch and Schn.

*Location of Parasite in Host:* Intestine.

Hosts obtained from Hobart fish market, May, 1945.

*Discussion:* The sub-family *Prosorhynchinae* was set up by Ohdner (1905), to include *P. squamatus* Ohdner, *P. crucibulum* (Rud.) and *P. aculeatus* Ohdner. The essential features of Ohdner's diagnosis are the presence of a rostellum and the configuration of the yolk follicles in the form of an anterior arc, or convex bow, in the fore-body. Many species have been admitted to the sub-family which possess an attachment organ in the form of a rostellum or rhynchus, but which have the vitellaria arranged in two lateral groups not fusing anteriorly. The presence of an attachment organ in the form of a muscular rhynchus has remained the distinguishing feature of the sub-family. Within the group there is much confusion and disagreement between workers as to the validity of various species and genera. As Manter (1940) remarks, such confusion "invariably accompanies the early taxonomic history of a group which is being rapidly expanded".

The species most closely related to the form described above are found within the genera *Prosorhynchus* Ohdner, and *Skrjabiniella* Issaitschikow (the latter not accepted as a valid genus by some workers). The genus *Skrjabiniella* was set up for *Prosorhynchus aculeatus* on the basis of the testes being on either side of the body, the mouth being situated in the posterior half of the body, and the uterus not extending anteriorly to the vitellaria. Manter (1934) does not consider these characters to be of generic importance and regards *Skrjabiniella* as a synonym of *Prosorhynchus*. Jones (1943), however, would show the validity of *Skrjabiniella* by arranging eleven species of *Prosorhynchus* into two groups upon five characters which she regards as of generic importance, viz., the shape of the body (whether elongate or oval), the arrangement of the testes (in tandem or symmetrically on either side of the body), the shape of the rhynchus (conical or oval), the position of the mouth relative to the anterior testis (anterior or posterior) and the arrangement of the vitellaria (in two separated lateral groups or in an anterior convex arc). Jones shows that the eleven species, with two exceptions, fall into two groups upon all five characters. *P. aculeatus* Ohdner, *P. squamatus* Ohdner, *P. uniporus* Ozaki and *P. grandis* Lebour are placed within the

genus *Skrjabiniella*, while the remaining species dealt with, viz., *P. facilis* (Ozaki), *P. cortai* Trav., Art. and Per., *P. platycephali* (Yamaguti), *P. manteri* Sriv. and *P. arabiana* Sriv. are placed within the genus *Prosorhynchus s. str.* This scheme breaks down when further species are considered, e.g., *P. rotundus* Manter 1940 falls into the genus *Skrjabiniella* upon body shape, but in *Prosorhynchus s. str.* upon the remaining four criteria adopted by Jones; *P. gonoderus* Manter 1940 resembles *Prosorhynchus s. str.* in its elongate form and conical rhynchus, but has the testes arranged in the manner characteristic of *Skrjabiniella* species. It appears, therefore, that a separation of the two genera based upon five characters is unsatisfactory, especially as such characters as the form of the body and the positions of the testes relative to one another and to the position of the mouth are sometimes difficult to determine in highly extensible forms.

It must be remembered that if the nature of the configuration of the yolk follicles is to be used as a means of dividing *Prosorhynchus* Ohdner into two genera, those species which conform with Ohdner's generic diagnosis, viz., *P. aculeatus*, *P. squamatus*, *P. uniporus* and *P. grandis*, should remain in the genus *Prosorhynchus*.

The use of the configuration of the yolk follicles as a feature of diagnostic importance has received much attention in the Bucephalidae. Issaitschikow (1928) attempts to divide the family into two sub-families upon this character. Pigulewsky (1931) regards the configuration of the yolk follicles as a means of dividing the sub-family *Prosorhynchinae* Ohdner into two tribes, *Prosorhynchia* and *Gotonia*. The validity of *Gotonius* Ozaki has not been accepted by subsequent writers with the exception of Yamaguti, who described *Gotonius platycephali*.

The form of the attachment organ remains an important diagnostic character within the Bucephalidae. As two distinct types of rhynchus occur in different *Prosorhynchus* species, it seems possible that any natural cleavage within the genus will emerge upon consideration of the nature of the rhynchus and the configuration of the yolk follicles. In the following table the known species of *Prosorhynchus* are listed and the form of the rhynchus and the configuration of the yolk follicles stated in each case:

Group I.		
<i>P. aculeatus</i> Ohdner	Yolk follicles in an anterior arc.	Rhynchus oval.
<i>P. squamatus</i> Ohdner	"	"
<i>P. uniporus</i> Ozaki	"	"
<i>P. grandis</i> Lebour	"	"
Group II.		
<i>P. facilis</i> Ozaki	Yolk follicles in two lateral groups.	Rhynchus tapered internally.
<i>P. cortai</i> Trav., Art. & Per.	"	"
<i>P. platycephali</i> (Yamaguti)	"	"
<i>P. manteri</i> Sriv.	"	"
<i>P. arabiana</i> Sriv.	"	"
<i>P. ozakii</i> Manter	"	"
<i>P. rotundus</i> Manter	"	"
<i>P. gonoderus</i> Manter	"	"
<i>P. pacificus</i> Manter	"	"
<i>P. atlanticus</i> Manter	"	"
<i>P. promicropsi</i> Manter	"	"

The natural cleavage into two groups is probably sufficient evidence for assuming the presence of two genera. As indicated above, the proposal to regard the species listed in Group I as members of a genus other than *Prosorhynchus* is not permissible. If any species are to be removed from the genus *Prosorhynchus* Ohdner they should be the members of Group II. The writer, therefore, does not regard *Skrjabiniella* as a valid genus.

The genus *Gotonius* Ozaki is the most suitable genus to receive the members of Group II above. Srivastava (1938) attempts to show that *Prosorhynchus* and *Gotonius* are synonymous. However, this conclusion is based upon comparisons of body shape and relative positions of the gonads, neither of which characters can be regarded as a sound basis for comparison in this group.

As *Telorhynchus arripidis*, n. gen., n. sp., possesses a conical rhynchus and yolk follicles in the form of an anterior arc, it is regarded as a linking form. It differs from the species listed above in that the rhynchus is armed with a single circlet of spines, interrupted in the mid-ventral line.

Two members of the *Prosorhynchinae* possessing rhynchal spines have been described, viz., *Dolljustrrema vaneyi* (Shen) and *Dolljustrrema gravidum* Manter, which have a triple row of spines. The writer considers Manter (1940) mistaken in assuming that the spines of *Dolljustrrema* correspond to the cuticular folds upon the rhynchus of *Mordvilkovia* Pigulewsky. The cuticular folds shown in Pigulewsky's illustration do suggest irregularly arranged spines but this resemblance seems insufficient reason to assume the synonymy of the two genera. *Mordvilkovia* is regarded as a valid genus.

Family ALLOCREADIIDAE.

Sub-family ALLOCREADIINAE.

Genus HELICOMETRA Ohdner.

HELICOMETRA NEOSEBASTODIS, n. sp.

*External Features:* The body is elongate, being broadest at about the middle length, and tapering towards the extremities. The body is flattened dorsoventrally, especially in the posterior region, which is leaf-like, possessing frilled or convoluted lateral margins. Both anterior and posterior regions of the animal are highly extensible. Specimens fixed under slight cover-glass pressure measure 3.02–5.9 mm. long and 0.7–1.0 mm. broad.

The oral sucker is subterminal, and is relatively large for the genus, measuring 0.31–0.49 mm. in diameter. It tapers towards the prepharynx and has a longitudinally-elongated aperture. The acetabulum is situated at the junction of the first and second quarters of the body length and measures 0.29–0.46 mm. in diameter. In each of the ten "in toto" mounts, the acetabulum was slightly smaller than the oral sucker. The

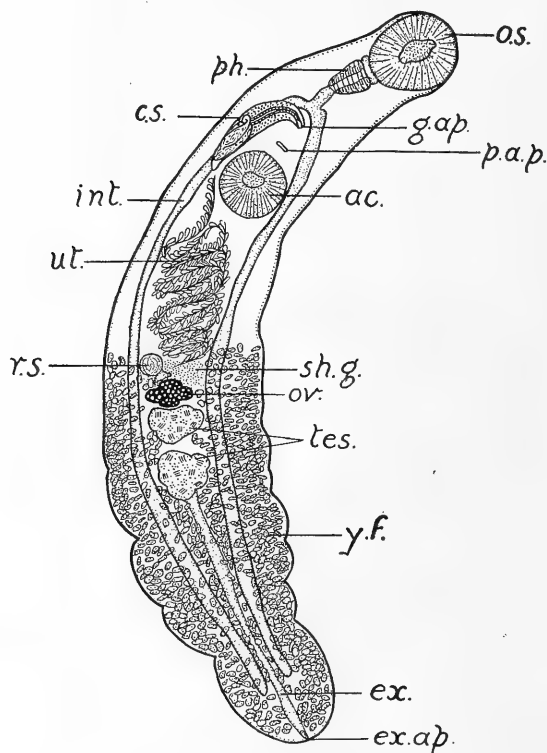


Fig. 6.—*Helicometra neosebastodis*, n. sp. Whole animal from the ventral aspect.

common genital aperture is situated on the ventral surface in the mid-line, midway between the suckers. There is a transversely-elongated aperture, the entrance to a deep pit, equidistant between the genital aperture and the anterior edge of the acetabulum. The excretory pore is situated in a depressed groove on the dorsal surface, near the posterior extremity. The cuticle is smooth and spineless. As in *Helicometra tenuifolia* Woolcock there are numerous short finger-like sub-cuticular canals opening on the surface by minute pores. These canals are especially prominent along the lateral margins of the body and about the border of the oral sucker. As suggested by Woolcock (1937), they are probably excretory in function.

*Digestive System:* The cavity of the oral sucker leads through a short thin-walled prepharynx into the muscular pharynx. This measures 0.16–0.19 mm. long and is of the same measurement in width anteriorly, but tapers posteriorly. The pharynx is connected to the gut rami by a muscular oesophagus of the same length as the pharynx. The wall of the oesophagus contains stout outer longitudinal muscles and weaker inner circular muscles. The gut rami diverge from the posterior end of the oesophagus and run backwards on either side of the cirrus-sac as sinuous tubes, somewhat irregular in transverse section. The walls of the rami are fairly muscular, possessing muscles similar to those of the oesophagus. The rami are lined by an epithelium of flattened cells containing large ovoid nuclei. Posterior to the acetabulum, the rami are situated a considerable distance from the lateral margins of the body, and extend in this position almost to the posterior extremity. The gut is not connected with the excretory vesicle.

*Excretory System:* The excretory vesicle is a long slender tube which extends from the excretory pore to the uterine region and in position is dorsal to the testes and ovary. Anteriorly the vesicle does not terminate blindly, but breaks up and diffuses into the regular spongy parenchyma which fills the body between the coils of the uterus. The vesicle does not extend further forward than the middle of the uterine region. At the

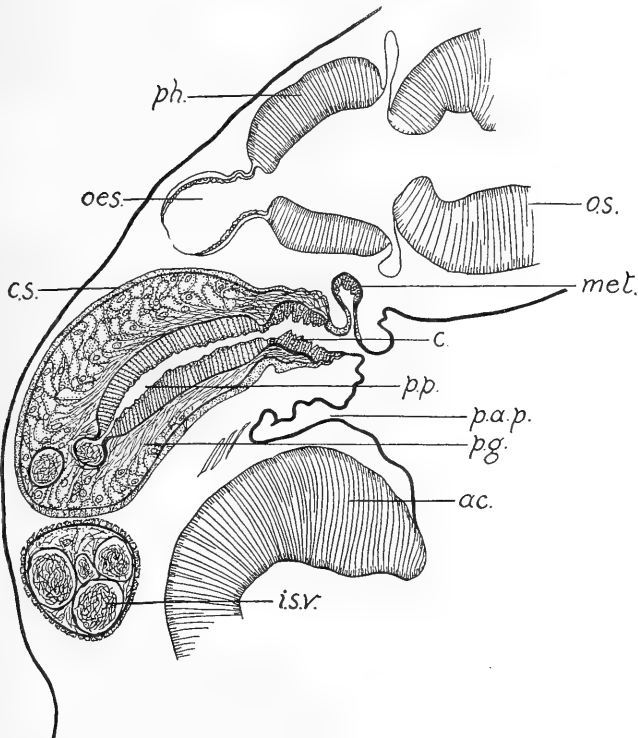


Fig. 7.—*Helicometra neosebastodis*, n. sp. Portion of sagittal section showing cirrus-sac and male duct.

level of the receptaculum seminis, a lateral duct is given off on either side, and runs obliquely forwards and outwards coming to lie on the inner side of the gut. The lateral ducts extend into the neck region as far as the pharynx, where each terminates in a slightly expanded chamber containing a large multi-ciliar flume.

*Genital System—Male:* The two testes are in tandem and situated in the intercaecal space within the third quarter of the body. They are roundly indented and variable in outline. In the largest mounted specimen, which is 5.9 mm. in length, the testes measure  $0.39 \times 0.26$  mm. and  $0.33 \times 0.3$  mm. respectively. The slender vasa deferentia leave the mid-dorsal surfaces of the testes and run forwards together dorsal to the ovary. They then diverge and pass on either side of the helical uterus, lying just within the intestinal rami. The vas deferens from the anterior testis lies on the left side, that of the posterior testis on the right. Immediately posterior to the acetabulum the vasa deferentia converge and pass together to the rear end of the cirrus-sac. They enter the cirrus-sac through its ventral surface a little in front of its posterior end, and immediately open into the large longitudinally-coiled seminal vesicle which occupies its posterior half. The cirrus-sac is large and well developed, measuring as much as 0.14 mm. in diameter and extending from the genital pore to the level of the middle of the acetabulum. It is banana-shaped, being curved and tapered towards either end; it lies generally in the mid-line, but is displaced to the left side in mounted or flattened specimens. The sac wall is highly muscular, consisting of thin inner circular and stout outer longitudinal muscles. Near its anterior end the cirrus-sac is connected with the ventral body wall by stout lateral oblique muscles which probably aid the protrusion of the cirrus by drawing the cirrus-sac towards the ventral surface.

The internal seminal vesicle has a thin membranous wall, which contains widely separated nuclei. Anteriorly the vesicle is constricted and leads through a sphincter into the well-developed pars prostatica. This section of the male duct possesses a thin membranous wall lined by large columnar vacuolate cells in which no nuclei are visible. Anteriorly the pars prostatica narrows and passes into the short broad muscular cirrus, which extends to the anterior limit of the cirrus-sac. The male duct now meets the metraterm, the muscular wall of the two ducts being continuous, and forms a short narrow common genital atrium leading to the exterior.

*Genital System—Female:* The ovary is situated in the mid-line, immediately in front of the anterior testis and sometimes contiguous with it. The ovary is characteristically four-lobed, in the form of a transversely elongated four-leafed clover and measures 0.08–0.19 mm. long and 0.29 mm. broad. The ripe ova within the anterior lobe of the ovary measure up to 0.008 mm. in diameter. The oviduct arises at the anterior border of the ovary and runs upwards a distance of 0.08 mm. to enter the ventral surface of the receptaculum seminis. The proximal portion of the oviduct is very narrow. This expands into a broader ciliated division leading to the receptaculum seminis. The latter is spherical or pear-shaped, depending on the degree of distension, and measures in two sectioned specimens approximately 0.13 mm. in diameter. The wall of the receptaculum is membranous and contains large flattened nuclei. The receptaculum is usually situated to the left of the mid-line directly in front of the ovary, but it is occasionally median and directly dorsal to that organ. Anteriorly it is drawn out into Laurer's canal, which passes forwards and upwards as a thick-walled convoluted tube approximately 0.008 mm. in diameter, and opens on the dorsal surface to the left of the mid-line.

A broad duct leaves the receptaculum seminis immediately in front of the entrance of the oviduct and passes towards the ventral surface for a short distance. It then turns upon itself and expands into the ootype. The thick wall of the ootype is surrounded by innumerable radiating threads derived from the cells of the shell gland. The shell gland is exceptionally large and diffuse, surrounding the female complex and filling most of the intercaecal space in front of the ovary. The gland cells are most profuse laterally. They are large with uniformly staining contents and possess large vacuolate nuclei. After receiving a slender duct from the yolk reservoir the uterus forms a helix of eight or nine loops containing several hundred eggs between the shell gland and the acetabulum. The uterine coils enclose a core of spongy parenchyma.

Immediately behind the acetabulum the membranous wall of the uterus, containing widely separated flattened nuclei, abruptly changes into the thin muscular wall of the metraterm composed of weakly-developed inner circular and outer longitudinal muscles. The metraterm passes over the acetabulum on the left side and then forwards closely appressed to the cirrus-sac. It then passes from a lateral position on the left side of the cirrus-sac to a dorsal position at its anterior end. The metraterm may extend beyond the level of the genital pore before turning downwards to open into the common genital atrium directly in front of the male aperture.

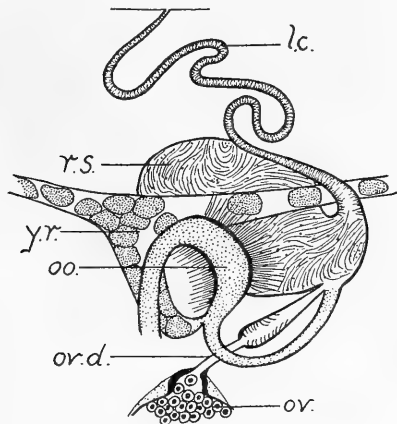


Fig. 8.—*Helicometra neosebastodis*, n. sp. Diagram of female complex, drawn from transverse sections. Shell gland omitted for clarity.

The eggs are light orange-brown, and measure 0.06–0.068 mm. long, and 0.02–0.028 mm. broad. At one end the shell is drawn out into a long, hollow, tapering filament which measures six or seven times the length of the egg. At the opposite end of the egg there is an operculum. As the eggs are arranged in close succession, with their filaments tapering behind, a section through the uterus at any point shows a number of the filaments cut through at different levels. The egg-shell is a double structure consisting of a thin outer dense layer and a thick inner light-coloured layer. The vitelline follicles are small and variable in shape and size, varying from ovoid follicles measuring approximately  $0.08 \times 0.04$  mm. to spherical forms 0.028 mm. in diameter. The follicles are very numerous and extend from the posterior extremity to the level of the first two or three uterine loops. They lie above, below and outside the gut rami and fill the post-testicular intercaecal space. Fine tubules connect them on either side with anterior and posterior lateral yolk ducts which lie outside the rami. The lateral ducts fuse on either side into transverse ducts which run directly across the body immediately in front of the ovary. The two transverse ducts expand and fuse to form the yolk reservoir, to the right of the mid-line. A slender duct runs forward from the reservoir to the ootype.

**Muscular System:** The musculature of the reproductive organs has been described above. The entire body wall is strongly muscular, containing well-developed circular, longitudinal and oblique muscles, which are especially developed in the neck region. Dorso-ventral fibres are very numerous throughout the body. The suckers present no unusual features, containing the usual equatorial, meridional and radial fibres. The oral sucker possesses no distinct retractor muscles, but in connection with the acetabulum there are well-developed anterior and posterior oblique muscle bands running to the dorsal body wall in front of the preacetabular pit.

**Nervous System:** The pair of ganglia composing the brain lie towards the dorsal surface of the anterior end of the pharynx. They are composed entirely of nerve fibres possessing nuclei only around their periphery. The ganglia are connected above and below the pharynx by slender commissures. Stout nerves run directly to the dorsal and

ventral body surfaces on either side. The ganglia are continued posteriorly into paired nerve chords immediately within the excretory canals. These nerves were not traced backwards beyond the oesophagus.

*Host: Neosebastes thetidis* Waite.

*Location of Parasite in Host:* Gut immediately behind stomach.

*Degree of Infection:* One to three parasites in each of seven fish examined.

Hosts obtained from Hobart fish market, December, 1944.

*Discussion:* The species described above is most closely related to *Helicometra tenuifolia* Woolcock, from which it differs in the possession of lobed testes which are much smaller than the acetabulum, and in the size and relative proportions of the body. The locality and the host are also distinct.

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## OBSERVATIONS ON PROPERTIES OF CERTAIN FUNGICIDAL COMPOUNDS.

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(Plate iii.)

[Read 29th May, 1946.]

## INTRODUCTION.

Much research work has in recent years been devoted to the control of lower fungi and other micro-organisms causing spoilage of various industrial products, including materials such as cotton and woollen textiles, paper and cardboard, wood, leather, plastics, etc., which are used in several kinds of military equipment. It is common experience that such materials are liable to deteriorate in tropical regions where ecological factors are often very favourable for the growth of fungi. Many different methods of "mould-proofing" by treatment with fungicidal or fungistatic chemicals have been proposed, but an ideal fungicide suitable for universal use has not been found, and could hardly be hoped for, in view of the widely different nature of the materials to be treated and the probably equally variable character of the many kinds of organisms against which protection is sought.\* During the years 1942-44 the author has had occasion to test the usefulness of various chemical compounds as mould-proofing agents for materials used in military equipment. The present paper briefly summarizes the results of some of these tests on a number of fungi typical of the microflora found on materials that had undergone deterioration under conditions of tropical warfare.

## MATERIALS AND METHODS.

The tests comprised altogether 23 strains of fungi which may be divided into two broad groups according to their action.

Group A consists of the following species which caused actual decay and loss of strength of cellulosic fabrics:

- |  |                                      |
|--|--------------------------------------|
| (1). <i>Stachybotrys</i> sp., isolated from decayed sandbag. |                                      |
| (2) and (3). <i>Memnoniella echinata</i>                     | } isolated from decayed tent canvas. |
| (4). <i>Helminthosporium</i> sp.                             |                                      |
| (5). <i>Curvularia lunata</i>                                |                                      |
| (6). <i>Alternaria</i> sp., isolated from flax straw.        |                                      |
| (7). <i>Pestalozzia palmarum</i>                             | } isolated from decayed tent canvas. |
| (8). <i>Chaetomium fumicolium</i>                            |                                      |
| (9) and (10). Sterile mycelia                                |                                      |
| (11). <i>Actinomyces</i> sp.                                 |                                      |

The last species, although not really a fungus, was included on account of its considerable power of destroying cellulosic materials. This property was most strongly developed in *Stachybotrys* and *Memnoniella* which caused complete or almost complete loss of the tensile strength of 12-oz. cotton duck, placed on a mineral salts agar medium, after 7-14 days' incubation at 30°C. Moderately destructive were *Actinomyces*, Sterile Mycelium b, *Chaetomium*, *Curvularia*, and *Pestalozzia*, which caused from 50 to 80% loss of strength in 14 days. The remaining three species were less active, causing only about 10 to 30% loss of strength.

\* A general discussion of fungicides and their properties is given by Horsfall (1945).

Group B includes fungi which grew extensively on the surface of different materials but caused little or no decay of fabrics:

- (12). *Aspergillus niger*, from canvas treated with copper oleate.
- (13) and (14). *Aspergillus flavus*, the first (a) from mouldy leather, the second (b) from canvas treated with salicylanilide (laboratory experiment).
- (15)–(18). *Penicillium* spp., one (a) from a wireless set, two (b) and (c) from canvas treated with copper oleo-stearate, and one (d) from infected human blood serum with 0.01% merthiolate. The last strain was included because of its high resistance to mercurial antiseptics.
- (19). *Paecilomyces* sp., from canvas treated with copper tannate.
- (20)–(22). *Fusarium* spp., from untreated, mouldy tent canvas.
- (23). *Pestalozzia* sp., from mouldy leather.

Strains Nos. 1, 2, 7, 8, 11, 13 and 23 were isolated by Mr. G. C. Wade, Department of Agriculture, Melbourne, Vict., the rest by the author. Identification of the organisms is due to Dr. Lilian Fraser, Department of Agriculture, Sydney, N.S.W. The determinations of tensile strength of canvas were made by the Munitions Supply Laboratory, Melbourne and Sydney.

*Aspergillus niger* and *Penicillium a*, *b* and *c* showed a conspicuous reaction which has also been observed by Marsh *et al.* (1944): growth took place on canvas or filter paper impregnated with copper oleate, and was accompanied by complete loss of the deep green colour of the organic copper compound. Water-proofness of the canvas was completely destroyed in the decolourized areas. The phenomenon was apparently due to decomposition of the oleic acid radicle and reduction of the copper from the cupric to the cuprous state. Other fungi did not cause this loss of colour, although several of them grew readily on canvas treated with copper oleate. In agreement with Marsh *et al.* (1944) it was also found that no growth and colour reduction took place on material treated with copper naphthenate, apparently because the naphthenic acid radicle itself has a fungistatic action: 1.0 and 0.2% ammonium naphthenate in synthetic nutrient solution suppressed the growth of *Aspergillus niger* and *Penicillium* sp., respectively. Oleic and stearic acid, on the other hand, proved to be excellent sources of carbon for many of the fungi.

The following fungicidal compounds were tested:

- (a). Chlorine-substituted phenols: 2:4:6-trichlorophenol, 2:3:4:6-tetrachlorophenol, pentachlorophenol.
- (b). Other phenol-derivatives: *p*-nitrophenol, dinitro-ortho-cresol, salicylanilide.
- (c). Organic sulphur compound: sodium diethyldithiocarbamate.
- (d). Invert soap: Zephiran (alkyl-dimethyl-benzyl-ammonium chloride).
- (e). Organic mercury compound: phenylmercuric acetate.
- (f). Inorganic salt of heavy metal: copper sulphate.

All compounds were used in aqueous solution, the phenol derivatives as sodium salts. Some additional tests were made with a few other fungicides that did not form water-soluble compounds.

For the main experiments the fungi were grown in a semi-synthetic medium of the following composition: glucose 2.0%, asparagin 0.05%, ammonium lactate 0.2%,  $K_2HPO_4$  (or  $KH_2PO_4$ ) 0.05%,  $MgSO_4$  0.05%, NaCl 0.05%,  $FeCl_3$  0.01%, agar 0.3%. The basal medium supported good growth of even the more exacting fungi like *Stachybotrys* and *Memnoniella* within one week at 30°C.; many species produced abundant growth after 3 or 4 days. The fungicidal compounds to be tested were added in concentrations decreasing with approximately twofold steps of dilution, e.g., 1:1,000–2,000–5,000–10,000, etc. In order to avoid strong heating of the medium in the presence of the fungicide, the medium was first made up with 25% higher concentration of the constituents, sterilized by autoclaving, and cooled to about 60°C.; the required amount of fungicide was then added from a sterile stock solution, the reaction was adjusted, if necessary, with sterile sulphuric acid and sodium hydroxide, and sufficient sterile distilled water was added to give the desired final concentration of fungicide with constant concentration of nutrients; while still warm, the medium was distributed aseptically in 5-ml. portions

to sterile test-tubes. Each compound was tested at two ranges of reaction: pH 4.7-4.8 and pH 7.0-7.2. Duplicate cultures of each organism at each dilution of fungicide were inoculated and incubated at 30°C. Since the tests included fungi with conidia of very variable size, and some that grew only as mycelia, it was not practicable to standardize the inocula in terms of spore density per volume of suspension; a heavy inoculum was given in all cases, either as a just visible speck of conidia from a young agar culture, or as a similar tuft of vegetative mycelium. Weekly readings were taken of the growth during a period of three weeks, and the highest dilution that prevented growth within this time was taken as the limit of concentration of fungicide necessary for complete inhibition; only very rarely was any growth seen to develop after the second week of incubation. This method has certain advantages over the less time-consuming and more quantitative method of measuring the diameter of fungal colonies on agar medium in Petri dishes, in so far as it is more suitable for detecting delayed growth of the slowly growing fungi.

The results of the tests are seen in Tables 1-2, which give the fungistatic values of each compound towards the different fungi, as reciprocals of the highest dilution ( $\times 1,000$ ) that prevented growth during three weeks. Thus a value of 10 indicates no growth at a dilution of 1:10,000 or lower, but growth at 1:20,000 or higher. At the foot of each column the mean of these values is given as the "fungistatic index" of the compound at the two ranges of pH. For some of the compounds the dissociation exponent (pK, the negative logarithm of the dissociation constant) is also given, as well as the degree of ionization calculated by the formula

$$\% \text{ ionization} = \frac{100}{1 + \text{antilog}(\text{pK} - \text{pH})}$$

The pK values for trichlorophenol, *p*-nitrophenol and dinitro-ortho-cresol were taken from the data of Krahl and Clowes (1938), while the values for tetra- and pentachlorophenol and salicylanilide were determined by Mr. R. J. Goldacre, Department of Organic Chemistry, University of Sydney.

#### EXPERIMENTAL RESULTS.

The three chlorophenols are strongly fungistatic, especially at acid reaction; a similar effect of pH on the toxicity of trichlorophenol towards *Staphylococcus aureus* was observed by Ordal and Deromedi (1943). The difference in toxicity at the two pH ranges is most pronounced in pentachlorophenol which is the strongest acid and approximately half ionized in the acid medium. At neutral reaction the differences in ionization are only small, and also the differences in fungistatic activity are comparatively insignificant. Trichlorophenol appears the most toxic at neutral reaction, but being the weakest acid it also has the highest proportion of non-ionized molecules which appear to be more toxic than the ions—a phenomenon observed in many other instances, as discussed below. It also appears that the toxicity of the non-ionized molecules, but not of the ions, increases with the number of Cl-atoms and the acidic strength of the compound. A simple calculation may be made of the relative toxicity of ions and molecules. If we let *I* represent the fungistatic index of the ions and *M* that of the non-ionized molecules, we have for trichlorophenol, for instance, the equations:

$$\begin{aligned} \text{at pH 4.8: } & \frac{4 I}{100} + \frac{96 M}{100} = 100 \\ \text{and at pH 7.2: } & \frac{91 I}{100} + \frac{9 M}{100} = 26 \end{aligned}$$

Thus we find for the three compounds:

	<i>I</i>	<i>M</i>	Ratio <i>I</i> : <i>M</i>	pK
Trichlorophenol .. .. .	18	103	1 : 5.6	6.2
Tetrachlorophenol .. .. .	4	244	1 : 61	6.0
Pentachlorophenol .. .. .	14	454	1 : 32	4.7

These values, however, must be taken with some reservation, because the toxicity of the non-ionized molecules appears to vary with pH, as shown below.

TABLE 1A.  
Fungistatic Effect of Phenol Derivatives.

pK of compound .. ..	Trichlorophenol.		Tetrachlorophenol.		Pentachlorophenol.	
	6.2		6.0		4.7	
	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2
pH of medium .. ..	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2
Per cent. ionization .. ..	3-4	86-91	4-6	91-93	50-55	(> 99)
Fungistatic value towards Group A.						
<i>Stachybotrys</i> sp. .. ..	200	50	500	50	500	20
<i>Memnoniella echinata</i> a .. ..	200	50	200	20	200	20
"   "   "   b .. ..	200	50	200	20	200	20
<i>Helminthosporium</i> sp. .. ..	100	20	200	20	100	20
<i>Curvularia lunata</i> .. ..	50	20	100	10	100	10
<i>Alternaria</i> sp. .. ..	50	20	100	10	50	10
<i>Pestalozzia palmarum</i> .. ..	200	50	500	20	500	20
<i>Chaetomium fumicolum</i> .. ..	200	50	1000	50	500	20
Sterile mycelium a .. ..	200	50	200	50	500	20
"   "   "   b .. ..	50	20	100	20	50	10
<i>Actinomyces</i> sp. .. ..	200	50	1000	50	1000	50
Group B.						
<i>Aspergillus niger</i> .. ..	50	20	100	10	50	20
" <i>flavus</i> a .. ..	20	5	50	10	20	5
"   "   "   b .. ..	20	5	50	10	50	5
<i>Penicillium</i> a .. ..	20	10	50	10	50	20
"   "   "   b .. ..	20	10	50	50	50	10
"   "   "   c .. ..	20	10	50	10	50	20
"   "   "   d .. ..	100	20	100	20	200	10
<i>Paecilomyces</i> sp. .. ..	50	10	100	10	50	10
<i>Fusarium</i> sp. a .. ..	50	5	50	5	50	5
"   "   "   b .. ..	50	10	50	5	50	2
"   "   "   c .. ..	50	10	50	10	50	5
<i>Pestalozzia</i> sp. .. ..	200	50	500	20	500	20
Mean (Fungistatic Index)	100	26	230	21	212	15
Do. as millimolar concentration	0.051	0.195	0.019	0.204	0.018	0.248

*p*-Nitrophenol is less toxic than the chlorophenols, particularly at acid reaction where it is practically non-ionized. Also in its half-ionized state at neutral reaction it is less toxic, but the effect of reaction is less pronounced than in the chlorophenols; its non-ionized molecules appear only about twice as toxic as its ions.

Dinitro-ortho-cresol shows a very interesting behaviour. At neutral reaction, where it is almost wholly ionized, it has only a weak fungistatic effect, but this is increased nearly 80-fold at pH 4.7-4.8 where the compound is still largely ionized on account of its strong acidic character. Many of the cultures in neutral medium with concentrations of dinitro-*o*-cresol below the fungistatic limit showed a marked *partial* inhibition: the inoculum germinated and produced a colony which, however, soon ceased growth and remained very small. This phenomenon might have been due to beginning acidification of the medium and consequent rise in the concentration of the more toxic non-ionized molecules.

In the two nitro-substituted phenol derivatives, as in the chlorophenols, we find some evidence that the toxicity of the non-ionized molecules increases (but that of the ions decreases) with the acidic strength or with the number of chlorine-atoms and nitro-groups. In the same manner as above, we find:

	Toxicity of Ions.	Ratio I : M Molecules.	pK
<i>p</i> -Nitrophenol .. .. .	38	1 : 2	7.2
Dinitro- <i>o</i> -cresol .. .. .	1.3	1 : 265	4.4

TABLE 1B.  
Fungistatic Effect of Phenol Derivatives.

pK of compound .. ..	p-Nitrophenol.		Dinitro-ortho-cresol.		Salicylanilide.	
	7.2		4.4		8.1	
pH of medium .. ..	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2
Per cent. ionization .. ..	0.3-0.4	40-50	67-71	(>99)	(<0.1)	7-9
Fungistatic value towards						
Group A.						
<i>Stachybotrys</i> sp. .. ..	10	5	200	5	50	20
<i>Memnoniella echinata a</i> .. ..	10	5	100	1	20	20
"    " <i>b</i> .. ..	10	10	100	2	20	20
<i>Helminthosporium</i> sp. .. ..	10	10	200	2	50	20
<i>Curvularia lunata</i> .. ..	10	10	50	1	20	20
<i>Alternaria</i> sp. .. ..	10	10	20	1	*	20
<i>Pestalozzia palmarum</i> .. ..	10	10	200	1	20	20
<i>Chaetomium fumicolum</i> .. ..	10	10	100	1	50	20
Sterile mycelium <i>a</i> .. ..	10	5	100	1	50	20
"    " <i>b</i> .. ..	10	5	20	1	20	20
<i>Actinomyces</i> sp. .. ..	5	2	500	5	20	20
Group B.						
<i>Aspergillus niger</i> .. ..	5	5	20	0.5	10 (r)	10
" <i>flavus a</i> .. ..	5	2	10	0.5	*	5
"    " <i>b</i> .. ..	5	2	10	0.5	*	5
<i>Penicillium a.</i> .. ..	5	5	10	1	20	20
" <i>b</i> .. ..	5	5	20	1	20	20
" <i>c</i> .. ..	5	5	20	1	20	20
" <i>d</i> .. ..	5	5	20	0.2	20	20
<i>Paecilomyces</i> sp. .. ..	10	2	20	0.5	20 (r)	20
<i>Fusarium</i> sp. <i>a</i> .. ..	10	2	10	0.5	10	10
"    " <i>b</i> .. ..	5	2	20	1	10 (r)	10
"    " <i>c</i> .. ..	5	2	20	0.5	10	10
<i>Pestalozzia</i> sp. .. ..	10	10	500	1	20	20
Mean (Fungistatic Index)	7.8	5.6	99	1.3	(20)	17
Do. as millimolar concentration	0.92	1.28	0.051	3.89	(0.224)	0.277

\* Growth not completely inhibited at any concentration where precipitation of the salicylanilide took place; "(r)" indicates that the inhibitory effect receded at concentrations higher than the one stated.

If the principle holds generally that non-ionized molecules are more toxic than their ions, we should expect the fungistatic effect of pentachlorophenol and dinitro-*o*-cresol to be further increased at a pH-value about 3, where both compounds are but very slightly ionized. A supplementary test with two of the more resistant fungi showed this to be the case. The following results were found:

	Pentachloro-phenol.	Dinitro-ortho-cresol.
Per cent. ionization .. .. .	0.6	2.4
Fungistatic value against <i>Aspergillus niger</i> .. .. .	500	200
"    "    "    " <i>flavus a</i> .. .. .	200	100

The toxicity of both compounds is seen to be ten times higher than at pH 4.7-4.8 (Table 1), while the increase in proportion of non-ionized molecules is only two- to three-fold, and the molecules thus appear to be 3 to 5 times as toxic as at pH 4.7-4.8. Therefore, and because of the uncertainty in determining the end-point of the inhibitory effect, which may be either linear or parabolic, the relative toxicities of the ions and non-ionized molecules calculated above can only be regarded as tentative. The drastic effect of the increasing acidity must evidently be due to some effect on the fungal cell, such as permeability of the cell membrane, the state of ionization of the chemical groups of the protoplasm with which the phenol-derivatives react, or a synergistic effect between the

fungicides and the hydrogen ion concentration of the medium; the last possibility was suggested by the fact that the growth in the control medium, particularly of *Aspergillus flavus*, was less rapid and vigorous at pH 2·8 than at pH 4·8 and 7.

In a series of kationic antiseptics, viz., the acridine derivatives, Albert *et al.* (1945) found evidence that the inhibitory effect consists in a competition between acridine ions and hydrogen ions for places on some vital enzyme. The possibility must therefore be considered that the toxic effect of the phenol derivatives might not really be exerted by the non-ionized molecules but might be due to a similar competition between their anions and hydroxyl ions. A calculation of the ratio between molar concentration of phenol ions and hydroxyl ions at inhibitory concentrations of the various compounds did not, however, altogether support this hypothesis. We find, for instance, when we calculate these ratios at the concentrations corresponding to the mean fungistatic values in Table 1:

		Ratio of phenol-derivative-ions to OH-ions	
		at pH 4·8	at pH 7·0
Trichlorophenol	.. .. .	3200:1	1700:1
Tetrachlorophenol	.. .. .	1850:1	1880:1
Pentachlorophenol	.. .. .	154000:1	2500:1
<i>p</i> -Nitrophenol	.. .. .	5800:1	5100:1
Dinitro- <i>o</i> -cresol	.. .. .	642000:1	419000:1

There is indeed in four of the compounds a fairly constant ratio, i.e., the approximately 150-fold increase in hydroxyl ion concentration is accompanied by a comparable increase in the concentration of phenol-derivative ions when full inhibition of the growth takes place, but in the case of pentachlorophenol this rule breaks down entirely. Erratic figures are also seen if we calculate the same ratios corresponding to the inhibitory concentrations of pentachlorophenol and dinitro-*o*-cresol towards *Aspergillus niger* and *A. flavus* at three different reactions:

Compound.	Fungus.	Ratio of phenolic ions to OH-ions		
		at pH 2·8	at pH 4·8	at pH 7·0
Pentachlorophenol	<i>A. niger</i>	7100:1	65000:1	1800:1
"	<i>A. flavus</i>	18000:1	163000:1	7500:1
Dinitro- <i>o</i> -cresol	<i>A. niger</i>	97000:1	28000:1	102000:1
"	<i>A. flavus</i>	192000:1	56000:1	102000:1

Here again the constancy disappears, especially in the case of pentachlorophenol. Moreover, the competition hypothesis could only apply to chemical groups on the cell surface, since the hydrogen ion concentration of the cell-interior may be considerably different from that of the growth medium.

Salicylanilide is a very weak acid and is only slightly ionized even at neutral reaction. Its activity was, on the whole, moderately high and was little influenced by the reaction, except that some of the more resistant fungi were not completely inhibited even by a concentration of 0·2% at acid reaction, where the salicylanilide formed a crystalline precipitate when added in concentrations of 0·02% and more; apparently the amount remaining in solution was below the limit of tolerance of these fungi. A few other species showed the singular phenomenon that growth was completely inhibited by moderate concentrations (1:10–20,000), but at higher concentrations the growth reappeared. A possible explanation may be that the salicylanilide was rapidly precipitated in higher concentrations, while a state of supersaturation may have persisted at the lower concentrations. *Aspergillus flavus*, strain *b*, even gave evidence of ability to decompose the salicylanilide, as shown by cultivation on an agar medium of pH 4·4–4·6, containing 0·2% salicylanilide (added in NaOH-solution), 0·1% (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> and KH<sub>2</sub>PO<sub>4</sub>, 0·05% MgSO<sub>4</sub> and NaCl, and 2·0% agar. Petri dish cultures incubated for three weeks at 30°C. showed fungal colonies surrounded by clear zones in which the finely crystalline precipitate of salicylanilide had disappeared (Plate iii). No growth took place on a similar neutral medium where the salicylanilide remained in solution. A scant growth also developed in a nutrient solution corresponding to the acid agar medium, but containing no other organic compound than the salicylanilide, which thus seems to serve as an available, but certainly very unfavourable, source of carbon for this particular strain of *Aspergillus flavus*. The other salicylanilide-tolerant fungi produced no clear zones on the agar medium.

Sodium diethyldithiocarbamate was also tested, but showed very little fungistatic activity, especially in the acid medium where it appeared to undergo decomposition with precipitation of free sulphur. Concentrations of 0.1 to 1.0% were required to suppress growth at pH 4.7-4.8, and 0.02-0.05% at pH 7.0-7.2.

The results with the three kationic fungicides are seen in Table 2.

TABLE 2.  
*Fungistatic Effect of Kationic Antiseptics.*

pH of medium .. ..	Zephiran.		Phenylmercuric Acetate.		Copper Sulphate.	
	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2	4.7-4.8	7.0-7.2
Fungistatic value towards						
Group A.						
<i>Stachybotrys</i> sp. .. ..	20	50	5000	2000	2.0	0.5
<i>Memnoniella echinata</i> a ..	100	50	10000	2000	1.0	0.5
"   "   "   b .. ..	50	50	10000	1000	0.5	0.5
<i>Helminthosporium</i> sp. .. ..	50	50	10000	2000	0.5	0.2
<i>Curvularia lunata</i> .. ..	20	20	1000	1000	1.0	0.5
<i>Alternaria</i> sp. .. ..	20	20	3200	1000	0.5	0.5
<i>Pestalozzia palmarum</i> .. ..	5	20	10000	3200	0.2	1.0
<i>Chaetomium</i> sp. .. ..	10	50	2000	2000	1.0	0.5
Sterile mycelium a .. ..	50	50	2000	2000	0.5	0.2
"   "   "   b .. ..	20	50	1000	1000	1.0	0.5
<i>Actinomyces</i> sp. .. ..	100	100	3200	1000		
Group B.						
<i>Aspergillus niger</i> .. ..	2	20	3200	2000	0.05	0.2
" <i>flavus</i> a .. ..	1	10	1000	500	0.5	0.2
"   "   "   b .. ..	2	20	1000	1000	0.5	0.2
<i>Penicillium</i> a .. ..	50	50	500	200	0.1	0.05
"   b .. ..	20	20	200	500	0.2	0.05
"   c .. ..	20	50	500	200	0.1	0.05
"   d .. ..	5	20	100	20	0.05	0.1
<i>Paecilomyces</i> sp. .. ..	5	50	1000	500	0.025	0.1
<i>Fusarium</i> sp. a .. ..	20	10	2000	500	0.5	0.5
"   "   b .. ..	5	5	2000	500	0.5	1.0
"   "   c .. ..	10	20	2000	500	1.0	1.0
<i>Pestalozzia</i> sp. .. ..	10	50	10000	1000	0.2	0.5
Mean (Fungistatic Index)	26	36	3560	1114	0.54	0.46
Do. as millimolar concentration			0.00083	0.0026	74	87

Zephiran is a salt of a strong base and can be regarded as fully ionized at both reactions. At pH 7.0-7.2 it is a powerful fungicide which considerably exceeds the phenol derivatives, but at acid reaction its effect is somewhat lessened. A similar but much more pronounced influence of the reaction on its toxicity to *Staphylococcus aureus* was observed by Gershenfeld and Perlstein (1941).

Phenylmercuric acetate is by far the most toxic of the substances tested. Only one species of *Penicillium* is as resistant to this compound as to the chlorophenols, and another equally resistant *Penicillium* was later isolated from tent canvas treated with phenylmercuric acetate. It is noteworthy that this high specific resistance to mercury is not accompanied by any particularly high resistance to the other fungicides. The mean fungistatic value at pH 4.7-4.8 is seen to be about three times higher than at pH 7.0-7.2. Phenylmercuric hydroxide has been regarded as a strong base (Breyer, 1939), of which the acetate should be almost fully ionized at both reactions, but a determination by Mr. Goldacre showed a pK of only 3.9, which corresponds to an ionization of 11-14% at pH 4.7-4.8 and practically none at pH 7.0-7.2. The ions would thus appear to be about 16 to 20 times as toxic as the free-base; this is in harmony with the fact that the anti-bacterial effect of mercury bichloride is due to the mercury ions forming non-ionized

compounds with vital SH-groups (Fildes, 1940). Phenylmercuric nitrate also appears to react with the SH-groups of respiratory enzymes (Cook *et al.*, 1946).

A supplementary test with *Penicillium d* in medium adjusted to more acid reactions gave the following results:

pH of medium .. .. .	2.9	3.9	5.1	6.1
Fungistatic value of phenylmercuric acetate .. ..	500	200	100	100
Per cent. ionization .. .. .	91	50	7	0.6

The high toxicity of the phenylmercuric ions compared with the non-ionized base is again obvious.

Copper sulphate is seen to be a rather weak fungistatic agent which is not much influenced by the reaction, despite the fact that the higher concentrations of copper at neutral reaction were largely precipitated as hydroxide; similar results were found by Hoffmann *et al.* (1941) and Dagys and Kaikaryte (1943). The most resistant fungus, *Paeclilomyces* sp., would still grow feebly at acid reaction in the presence of 2.0%, or 0.08 mol., CuSO<sub>4</sub>, H<sub>2</sub>O. None of the fungi thus show an extraordinary resistance to copper, such as certain others studied by Starkey and Waksman (1943) and earlier authors quoted by them.

It is noteworthy that the fabric-destroying fungi of Group A are upon the whole more sensitive to fungicides in general than the surface-growing species of Group B; the *Pestalozzia* in this group is the only striking exception to this rule. These results suggest that there may be a danger of misleading results in using only highly destructive but sensitive species like *Stachybotrys* or *Memnoniella* as test-organisms for rot-proofing of canvas and other cellulosic fabrics, because materials passing such a test might still be susceptible to attack by species less rapidly destructive on untreated material but more resistant towards fungicides.

Additional tests were performed on a smaller scale with a few compounds not soluble in water: tetramethyl- and tetraethylthiuramdisulphide, tetrachloroparabenzquinone (chloranil),  $\beta$ -naphthol and the insecticide dichlorodiphenyltrichloroethane (D.D.T.). Strips of filter paper, approximately 1 x 5 cm., were saturated with alcoholic solutions of the compounds in varying concentrations, dried at 96°C., and placed in Petri dishes on the surface of a sterile agar medium of the following composition: (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> 0.2%, KH<sub>2</sub>PO<sub>4</sub> 0.1%, MgSO<sub>4</sub> and NaCl 0.05%, agar 2.0%. The strips were inoculated at the centre with a loopful of spore suspension and incubated for one week at 30°C. Test organisms were *Stachybotrys* sp., *Memnoniella echinata* (b), *Actinomyces* sp., *Aspergillus niger*, *Asp. flavus* (b), and *Penicillium* sp. (b), which all grew well on control strips without fungicides. For comparison, several of the previously tested compounds which were soluble only as sodium salts, were re-tested by this method, also ethylmercurithiosalicylic acid, of which the water-soluble sodium salt is known as merthiolate. All tests were made in duplicate. The results are seen in Table 3.

The previously tested compounds appear in the same order of fungistatic activity as in Tables 1-2, although the fungistatic values are under these different conditions

TABLE 3.  
Fungistatic Effect of Compounds Applied to Filter Paper.

Compound.	Fungistatic Value towards Six Fungi.		
	Lowest.	Highest.	Mean.
Ethylmercurithiosalicylic acid .. ..	200	2000	550
Phenylmercuric acetate .. .. .	100	500	333
Pentachlorophenol .. .. .	1	20	5.8
Dinitro-ortho-cresol .. .. .	1	10	5.0
Tetramethylthiuramdisulphide (T.M.T.) .. ..	1	5	3.2
Tetraethylthiuramdisulphide (T.E.T.) .. ..	0.2	5	3.0
Tetrachlorobenzquinone .. .. .	0.5	5	1.6
Salicylanilide .. .. .	0.2	2	1.3
<i>p</i> -Nitrophenol .. .. .	0.2	1	0.7
$\beta$ -Naphthol .. .. .	0.5	0.5	0.5
Dichlorodiphenyltrichloroethane (D.D.T.) .. ..	<0.2	<0.2	(<0.2)



much lower (of the order of about one-tenth) than in the acid agar medium. Ethylmercurithiosalicylic acid even exceeds phenylmercuric acetate in toxicity. The two thiuramdisulphide-derivatives are effective fungicides which range between dinitro-*o*-cresol and salicylanilide, and chloranil is comparable to the latter compound.  $\beta$ -Naphthol is only a weak fungicide, and D.D.T. appears to have hardly any fungistatic properties at all, as also found by Norris (1945) and Horsfall (1945).

#### GENERAL CONCLUSIONS.

A common property of the phenol-derivatives is the tendency of their fungistatic activity to increase with increasing hydrogen ion concentration within the range in which their ionization is influenced, a phenomenon which suggests that the non-ionized molecules are more toxic than the ions. The same general rule has repeatedly been observed in experiments with several other anionic poisons towards both fungi and bacteria, for instance, by Vermast (1921) on benzoic acid towards *Bact. coli*, Cruess and Richert (1929) on the same compound towards several fungi, yeasts and bacteria, Reid (1932) on several aliphatic acids towards *Pseudomonas pyocyanea*, Levine and Fellers (1940) on acetic acid towards *Salmonella*, *Saccharomyces* and *Aspergillus niger*, Hoffmann *et al.* (1941) on benzoic and salicylic acid towards a mixed culture of fungi, Ordal and Deromedi (1943) on di- and trichlorophenol towards *Staph. aureus*, Dagys and Kaikaryte on acetic and salicylic acid towards *Absidia orchidis* and Rahn and Conn (1944) on benzoic and salicylic acid towards *Saccharomyces ellipsoideus*. The last authors, like Vermast (1921), showed that equitoxic solutions of sodium benzoate and sodium salicylate at different pH contained a constant concentration of non-ionized acid-molecules which alone appeared responsible for the toxic effect, and Krahl and Clowes (1938) found that the same applied to the toxicity of halogen- and nitro-substituted phenols to eggs of echinoderms. The higher toxicity of the non-ionized molecules has commonly been ascribed to the fact that they penetrate the cell membranes more readily than ions, but ionize inside the cell and react with vital chemical groups there (Robertson, 1945).

The present experiments with pentachlorophenol and dinitro-*o*-cresol did not show any constancy of non-ionized compound at inhibitory level, and the ions of all the phenol-derivatives showed more or less toxicity. It is therefore hardly possible to decide whether the increase in toxicity at increasing acidity is due to competition between phenolic anions and hydroxyl-ions combining with vital groups (enzymes) at the cell surface, or to formation of non-ionized molecules which show easier penetration of the cell membrane. In view of the irregular phenolic anion : hydroxyl-ion ratios, however, the second possibility would seem the more likely.

Dagys and Kaikaryte (1943) concluded from their experiments with *Absidia orchidis* that the effect of anionic poisons, e.g., acetic and salicylic acid, increases with increasing acidity, the effect of non-electrolytic poisons like ethyl alcohol and acetaldehyde is independent of the reaction, and the effect of kationic poisons increases with decreasing acidity. The last was found to apply only to mercuric bichloride and silver nitrate, and is not a general rule. Albert *et al.* (1945) found it applying to strongly basic but not to weakly basic acridines, of which the degree of ionization, and hence the bacteriostatic effect, increased with increasing acidity. In the present experiments the toxicity of phenylmercuric acetate, a salt of a weak base, was seen to be far less at pH 7.0-7.2 than at pH 4.7-4.8, which gave partial ionization of the base. The same has been found to apply to inorganic mercury compounds; thus Gershenfeld and Perlstein (1941) observed the bactericidal effect of mercuric bichloride on *Staph. aureus* to increase strongly as pH decreased from 7.4 to 4.0, and Hoffmann *et al.* (1941) found similar results with mixed fungal cultures. (Their statement that "substances such as mercuric chloride . . . are not markedly affected in their fungistatic action by a change in pH" seems contradicted by the data in their Table 1, which show that the inhibitory concentration of  $\text{HgCl}_2$  at pH 2 is five times as low as at pH 5, where it is again six times as low as at pH 7.)

Thus while the rule of Dagys and Kaikaryte can hardly be generalized, it might be tentatively suggested that phenol-derivatives, and perhaps also other anionic poisons, react with chemical groups in the cell interior and show increased activity at a hydrogen ion concentration which reduces their ionization, because of the greater ability

of the non-ionized molecules to penetrate the cell membrane. Ionization may take place inside the cell and the ions thus be ultimately responsible for the toxic effect which increases with the number of substituted Cl-atoms and NO<sub>2</sub>-groups. Kationic poisons such as acridines and mercury compounds, on the other hand, seem to react with groups on the cell surface and to be most active at a reaction giving maximal ionization, because they do not depend on ability to enter the protoplasm itself. In special cases the effect of pH would depend both on the strength of the kationic base and the nature of the groups with which it reacts, e.g., acridines act by competition with hydrogen ions, mercurial antiseptics by combination with sulphhydryl groups. In this connection it is noteworthy that the sulphhydryl groups of the dehydrogenases actually seem to be placed on the cell surface, as discussed by Robertson (1945).

#### SUMMARY.

Twenty-two species of fungi and one actinomycete, all typical representatives of the microflora found on organic materials attacked by mould growth under tropical conditions, were tested for their resistance to a number of fungicides.

Tri-, tetra- and pentachlorophenol, *p*-nitrophenol and dinitro-*o*-cresol were most active at acid reaction where the compounds were present as non-ionized molecules; the toxicity, and the acidic strength of the compounds, increased with the number of chlorine-atoms or nitro-groups. Salicylanilide proved inactive in certain cases where precipitation took place at acid reaction; a strain of *Aspergillus flavus* gave evidence of ability to decompose salicylanilide under certain conditions.

Zephiran, an invert soap, proved highly active at neutral reaction, somewhat less at pH 4.7-4.8. Phenylmercuric acetate was the most toxic of the compounds tested, especially at pH 4.7-4.8, where it was more ionized than at pH 7. The view is tentatively advanced that the substituted phenols act on chemical groups in the cell interior, but phenylmercuric acetate on sulphhydryl groups at the cell surface. Copper sulphate was comparatively little toxic, but none of the organisms showed an extraordinary resistance to copper.

Other tests indicated that tetramethyl- and tetraethylthiuramdisulphide and tetrachlorobenzoquinone had a fungistatic value similar to, or somewhat higher than, that of salicylanilide. Dichlorodiphenyltrichloroethane (D.D.T.) showed hardly any fungistatic power.

#### ACKNOWLEDGEMENTS.

The author's sincere thanks are due to Mr. R. J. Goldacre, M.Sc., Wellcome Research Fellow, Department of Organic Chemistry, for the determination of the dissociation constants, and to Dr. Adrien Albert for reading the manuscript and for numerous valuable suggestions and constructive criticism.

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## EXPLANATION OF PLATE III.

Colony of *Aspergillus flavus* on acid agar medium containing precipitate of salicylanilide. × 6.5. (Reg. Johnson photo.)

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AN OCCURRENCE OF RHYTHMIC BANDING IN ORDOVICIAN STRATA OF  
THE SHOALHAVEN RIVER GORGE.

By STEPHEN J. COPLAND, B.Sc.

(Plate v; two Text-figures.)

[Read 31st July, 1946.]

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I. DESCRIPTION OF THE BANDS.

Rhythmic banding expressed in strongly contrasted alternate light and dark bands is strikingly displayed in a section exposed on the right bank of the Shoalhaven River close to its junction with Diggers Creek, about two miles upstream from Badgery's Crossing, near Tallong. Rhythmic arrangement is maintained with great regularity over the series of 657 bands. The rock is an exceedingly fine sericite-biotite phyllite, which has been completely recrystallized. The strata with a deep water facies strike N. 8° W. and dip at an angle of approximately 83° towards the east. The almost vertical beds form the limb of an anticline which arches over towards the west, indicating that the lower beds are on that side. Sediments have undergone regional metamorphism at the close of the Ordovician and during other periods, and have also suffered contact metamorphism from association with the Marulan bathylith, which emerges at the surface little more than a mile away to the north-west, but which may approach more closely underground. The dark bands differ from the light in their high proportion of practically isotropic matrix, containing micaceous and carbonaceous material and chlorite. The difference in colour is chiefly due to concentration of pale brown biotite in parallel flakes, and to carbonaceous material. Parallelism of the biotite causes a marked lightening and darkening of the field when a section is rotated. The biotite, with the sericite, appears to be for the most part a product of weak metamorphism. Pressure acted practically entirely at right angles to the bedding planes so no rearrangement of the grains and flakes has occurred. Microscopic examination of the light bands shows no trace of carbonaceous material and this is borne out by the colour; whereas an analysis of the dark bands reveals a carbon content of 0.22 per cent. This amount must be considered significant. Harker (1932, p. 48) says: "Many black shales contain a noteworthy quantity of organic matter, and this is quickly affected by heating. Under a low pressure it may be wholly expelled, but more commonly it is reduced to graphite", and again (1932, p. 224): ". . . there are rocks sufficiently rich in graphite to assume a black colour, but not otherwise differing from the common types." Eight analyses of graptolite-bearing slates given by Joplin (1946, p. 162) show carbon as 0.04, 0.18, 0.38, 1.17, 1.51, 1.67, 1.88, and 2.15 per cent., one from near Tallong being 1.51. Both types of band contain small, glassy, rounded and subangular quartz grains, and even smaller angular ones; colourless, prismatic zircons, often with pyramidal ends and showing high relief and conchoidal fracture; rounded detrital grains and squat crystals of brown tourmaline; and rounded and squarish grains of magnetite and/or a titanium mineral.

Opinions on conditions at the time, by three students of the Ordovician, are quoted.

Sussmilch (1922, p. 30): "The waters of this sea appear to have been too deep for a shallow water fauna to flourish, but its surface waters were populated by a pelagic fauna in which graptolites were the dominant element. The nearest shore-line was too distant for any but the finer sediments to be transported to these regions and deposited. . . . The Ordovician was a period of considerable volcanic activity . . . immense quantities of volcanic ash were distributed far and wide."

David (1932, p. 39): "The large area of eastern Australia, lying generally to the east of this old shore-line ('. . . Barrier Ranges, thence east-south-east in the direction of Cobar, in New South Wales, thence southerly towards Narrandera, thence south-westerly . . .'), appears to have been a relatively deep sea. In Victoria there is a great development of Ordovician rocks of a pelagic graptolitic type belonging to this sea. These extend southwards into Tasmania, and northwards into New South Wales, right up to the Queensland Border."

Joplin (1946, p. 170) ends her comprehensive discussion with the summary: "It has been shown that the graptolite-bearing slates of the Upper Ordovician in New South Wales are highly siliceous and that their siliceous nature is probably original. It is suggested that they may have been formed as the result of large accumulations of volcanic ash which encased the plankton and prevented oxidation of the carbon content. This hypothesis for the origin of the graptolite-bearing black shales is considered in the light of other hypotheses and of the necessity to account for all the observed facts concerning black shale accumulation."

The series of 329 pairs of bands consists of three well-differentiated phases. In the lowest, Phase I, comprising pairs 1-100, the dark bands average about 0.8 in. in thickness and show little variation, while the light bands are very consistent at about 0.25 in. Apparently periods of rapid sedimentation were followed by long periods of quiet deposition. This phase of comparatively regular rhythmic alternation of conditions was upset during Phase II (pairs 101-183). Alternation of the bands persists, but the thickness of both types attains about 4 in. in thickness at the most irregular period. Here the deposition of sediment giving rise to the dark bands approached equality with that giving rise to the light. After 83 pairs of bands had given evidence of changed conditions, Phase III (pairs 184-329)—even more regular than the initial one—began and continued to the end of the series. In this phase of 146 pairs of bands, the light bands average approximately 0.2 in. in thickness and the dark are in the ratio of about three to one to them. The series thus begins and ends with similar phases separated by an irregular phase. These three periods probably represent a major cycle superimposed on the minor cycle represented by the 329 pairs of bands. The rounded and detrital nature of the minerals, the total absence of lithic grains even much decomposed, the fineness of the sediments, the fauna, and the character of the associated strata indicate that deposition occurred some distance from the shoreline.

It seems most improbable that the smaller rhythms are annual because deep-water conditions of sedimentation would preclude the laying down of such comparatively thick bands. Again, a detailed examination of the light bands frequently reveals as many as a dozen thin layers of dark material through each, although others are quite homogeneous. Similarly there may be thin layers of light material in a dark band. This minor layering is inconspicuous when compared with the boldly contrasted light and dark bands of the larger rhythm.

Complete measurements of the entire series of bands are given in Table 1. Their variations in thickness and ratio to each other are illustrated in two graphs (Figs. 1 and 2).

## II. DISCUSSION.

I have to thank Professor L. A. Cotton for the suggestion that Kindle's experimental work on the deposition of sediments might throw light on the formation of the rhythmic bands. Kindle (1917, pp. 906-909) found that in fresh water, sand and other coarse sediment settle first, followed by silt and fine particles; but in salt water silts may behave colloiddally, flocculate, and sink first, causing coarse layers to overlie the finer.

TABLE 1.

Table showing Thickness of All Bands, measured in Inches from the West (Earliest Beds). Light Bands are printed in Italics.

No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.	No. of Band.	Width of Band.
1	1.7*	43	0.2	84	0.2	125	1.6	166	4.7	207	0.1	248	0.2	289	0.1
	2.2		1.0		0.5		3.3		8.4		0.2		0.3		0.3
2	0.2	44	0.3	85	0.4	126	1.1	167	2.9	208	0.2	249	0.3	290	0.1
	1.4		0.5		0.8		1.0		1.5		0.4		0.5		0.6
3	0.2	45	0.2	86	0.3	127	0.9	168	2.0	209	0.2	250	0.2	291	0.1
	1.5		0.5		0.5		2.5		1.3		0.2		0.4		1.0
4	0.2	46	0.2	87	0.3	128	1.4	169	2.3	210	0.3	251	0.2	292	0.2
	0.6		1.0		0.5		2.9		4.0		0.4		0.5		0.4
5	0.1	47	0.3	88	0.3	129	1.9	170	4.5	211	0.2	252	0.2	293	0.1
	1.1		1.1		0.6		0.8		3.1		0.4		0.4		0.5
6	0.2	48	0.2	89	0.2	130	1.2	171	5.1	212	0.1	253	0.2	294	0.1
	1.1		1.0		0.9		1.5		3.3		0.3		0.5		0.5
7	0.3	49	0.2	90	0.2	131	0.9	172	4.7	213	0.3	254	0.1	295	0.1
	0.9		1.1		1.0		2.0		2.9		0.3		0.3		0.4
8	0.3	50	0.1	91	0.4	132	0.9	173	3.0	214	0.2	255	0.1	296	0.1
	0.9		0.3		1.1		2.2		4.2		0.4		0.4		0.6
9	0.3	51	0.2	92	0.2	133	1.4	174	2.1	215	0.2	256	0.1	297	0.1
	8.2*		0.6		1.6		2.3		1.1		0.2		0.3		0.6
10	0.2	52	0.3	93	0.3	134	4.4	175	7.7	216	0.2	257	0.1	298	0.1
	0.7		0.5		0.7		1.7		1.7		0.4		0.2		0.7
11	0.3	53	0.2	94	0.4	135	1.2	176	2.0	217	0.2	258	0.1	299	0.1
	1.0		0.8		0.7		2.0		1.5		0.5		0.2		0.9
12	0.3	54	0.3	95	0.3	136	2.0	177	2.4	218	0.1	259	0.1	300	0.1
	1.1		1.3		0.6		2.5		1.1		0.3		0.3		1.2
13	0.6	55	0.2	96	0.3	137	4.1	178	2.1	219	0.2	260	0.1	301	0.2
	0.2		0.9		0.4		2.1		4.0		0.2		0.3		0.7
14	0.2	56	0.2	97	0.5	138	2.1	179	3.1	220	0.2	261	0.2	302	0.2
	1.1		0.6		1.0		1.9		2.2		0.3		0.4		0.6
15	0.2	57	0.3	98	0.6	139	0.8	180	7.2	221	0.1	262	0.2	303	0.1
	0.9		1.1		0.6		2.8		2.6		0.3		0.2		0.7
16	0.2	58	0.2	99	0.2	140	1.3	181	2.1	222	0.1	263	0.1	304	0.2
	0.9		0.6		0.5		2.0		0.7		0.2		0.3		1.1
17	0.2	59	0.4	100	0.5	141	5.8	182	0.8	223	0.3	264	0.1	305	0.2
	1.0		0.7		0.6†		4.7		1.6		0.2		0.2		0.6
18	0.2	60	0.3	101	0.3	142	1.9	183	0.6†	224	0.2	265	0.1	306	0.1
	1.7		0.6		1.6		3.5		1.1		0.2		0.2		0.9
19	0.2	61	0.4	102	2.3	143	3.8	184	0.3	225	0.2	266	0.1	307	0.4
	0.4		1.0		1.0		2.4		0.9		0.3		0.2		1.0
20	0.2	62	0.3	103	0.5	144	1.5	185	0.3	226	0.1	267	0.2	308	0.2
	0.7		0.5		0.5		3.4		0.4		0.3		0.7		1.0
21	0.1	63	0.4	104	0.6	145	3.1	186	0.3	227	0.2	268	0.2	309	0.3
	0.4		0.4		0.5		3.4		0.1		0.3		0.2		0.2
22	0.2	64	0.2	105	0.9	146	1.4	187	0.3	228	0.2	269	0.1	310	0.2
	0.4		0.4		1.0		2.1		0.3		0.6		0.4		0.2
23	0.2	65	0.2	106	0.5	147	1.5	188	0.3	229	0.2	270	0.2	311	0.1
	0.7		1.0		1.3		2.7		0.4		0.2		0.4		1.1
24	0.3	66	0.2	107	0.7	148	1.5	189	0.2	230	0.2	271	0.2	312	0.2
	0.7		0.7		0.9		4.1		0.3		0.5		0.2		0.6
25	0.2	67	0.2	108	0.7	149	9.0	190	0.3	231	0.2	272	0.2	313	0.2
	0.6		0.6		1.1		5.3		1.0		0.3		0.4		0.9
26	0.2	68	0.2	109	0.8	150	2.6	191	0.2	232	0.2	273	0.2	314	0.2
	1.0		0.6		1.6		6.3		0.3		0.4		0.4		1.1
27	0.3	69	0.6	110	1.5	151	1.9	192	0.2	233	0.1	274	0.2	315	0.2
	0.6		2.0		1.5		3.0		0.3		0.6		0.3		1.1
28	0.3	70	0.2	111	0.8	152	5.9	193	0.2	234	0.2	275	0.1	316	0.3
	0.5		0.9		1.4		3.1		0.5		0.3		0.6		1.0
29	0.2	71	0.2	112	1.4	153	3.1	194	0.2	235	0.2	276	0.2	317	0.2
	0.7		1.0		0.9		2.8		0.3		0.5		1.1		1.1
30	0.2	72	0.2	113	0.7	154	4.2	195	0.2	236	0.2	277	0.1	318	0.1
	0.7		0.6		1.1		4.2		0.6		0.4		0.2		1.2
31	0.2	73	0.3	114	1.2	155	9.2	196	0.2	237	0.2	278	0.2	319	0.1
	0.7		1.0		0.6		6.7		0.5		0.3		0.6		1.1
32	0.2	74	0.2	115	0.7	156	4.1	197	0.2	238	0.2	279	0.1	320	0.2
	0.5		0.6		1.1		2.8		0.3		0.4		0.4		1.3
33	0.3	75	0.4	116	0.7	157	2.1	198	0.2	239	0.1	280	0.1	321	0.2
	0.5		1.0		1.8		1.4		0.4		0.5		0.7		0.8
34	0.2	76	0.3	117	0.7	158	2.3	199	0.1	240	0.2	281	0.2	322	0.2
	1.0		1.2		0.7		8.0		0.4		0.4		0.5		1.0
35	0.2	77	0.4	118	0.9	159	6.1	200	0.2	241	0.1	282	0.2	323	0.2
	1.2		1.2		0.9		14.7*		0.4		0.1		0.4		1.4
36	0.2	78	0.2	119	0.6	160	1.8	201	0.2	242	0.1	283	0.2	324	0.3
	1.4		0.6		1.6		1.8		0.4		0.5		0.5		0.8
37	0.2	79	0.2	120	1.0	161	2.2	202	0.2	243	0.2	284	0.2	325	0.2
	0.5		0.6		1.7		8.0		0.5		0.9		0.5		1.7
38	0.2	80	0.2	121	0.8	162	1.6	203	0.2	244	0.1	285	0.2	326	0.1
	1.3		1.7		2.6		2.6		0.8		0.6		0.5		1.7
39	0.2	81	0.3	122	0.6	163	3.1	204	0.3	245	0.2	286	0.1	327	0.3
	0.5		0.8		1.9		4.7		0.5		0.2		0.3		0.8
40	0.2	82	0.2	123	0.4	164	2.3	205	0.2	246	0.1	287	0.1	328	0.2
	0.5		0.9		0.8		1.7		0.3		0.4		0.4		0.9
41	0.2	83	0.3	124	0.8	165	1.9	206	0.3	247	0.3	288	0.1	329	0.2
	0.6		0.8		1.9		2.7		0.2		0.2		1.0		?

\* Obscured.

† Change from Phase I to Phase II.

‡ Change from Phase II to Phase III.

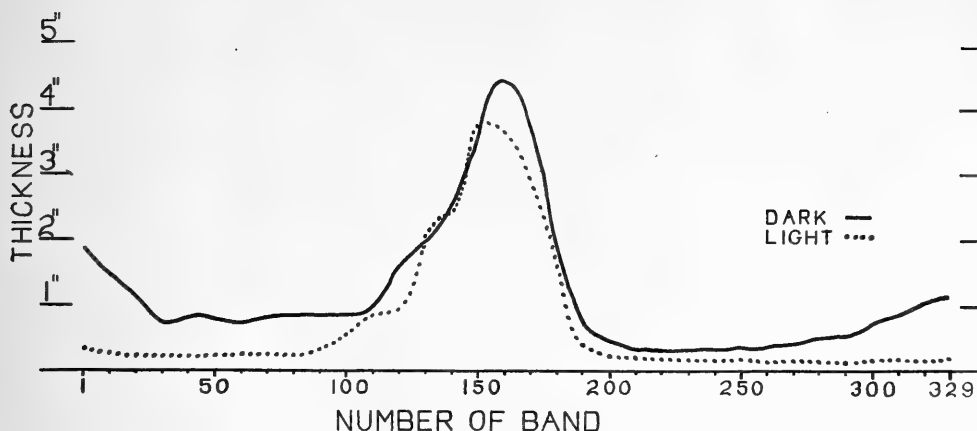


Fig. 1.—Graph showing the thickness of the light and of the dark bands. The end periods are separated by a phase of greatly increased sedimentation. The light bands are more regular in thickness than the dark, and are thinner except in the middle phase where irregular conditions bring both types into practical equality. Curves in both this and the following graph have been smoothed out by averaging small groups instead of single bands.

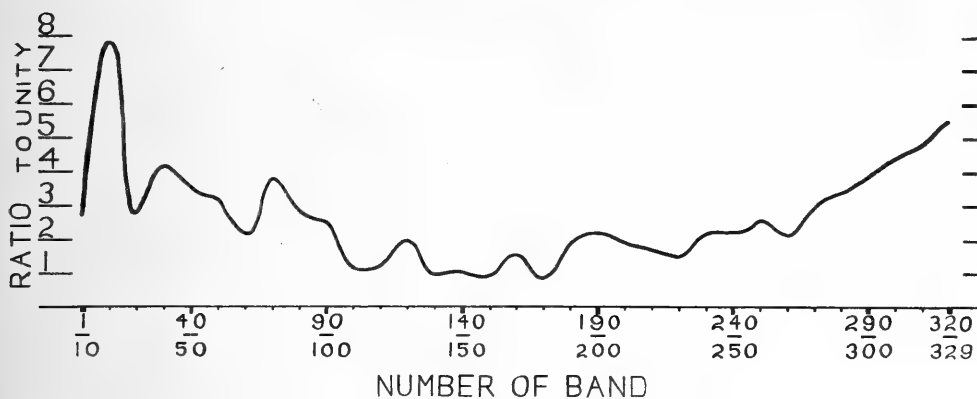


Fig. 2.—Graph showing the ratio in thickness of the dark to the light bands. The rising of the curve at each end represents quiet and regular conditions in the initial and final phases, and its bending down in the centre, the period when the balance of the end phases was upset by greatly increased and more irregular sedimentation. The sharp rise at the beginning of the series should be disregarded because it takes into account the thick 9th dark band (8.2 in.)—one of the very few which are doubtful and obscure, as indicated by asterisks in Table 1. It may include a number of both types of band.

Barrell (1917, p. 803) describes very regular thick bands of dark slate separated by thin bands of light shale containing a higher percentage of sand at Slatedale, Pennsylvania. He says: "Kindle has shown . . . in salt water the coagulation into nuclei is such that the slimes are deposited first, and the very fine sand follows"; "the ribbons often consist of a band of soft black mud-rock overlain by a band of nearly clean sand. The mixture of the two would appear to give the normal composition shown in the intervening beds." Then, adopting Kindle's explanation that storms have disturbed the sediments, he says: "the ribboned slates indicate, consequently, that at recurring intervals, the bottom of a shallow Ordovician sea was stirred up by waves of unusual intensity."

Twenhofel (1932, pp. 612-618) surveys the field, instancing weather changes (such as falls of rain or snow and storms), seasonal changes (as winter and summer), biological changes (as seasonal decomposition of vegetation), climatic cycles (as the 35-year cycle of Bruckner, the 21,000-year cycle of the precession of the equinoxes, and

the 91,000-year cycle of minimum and maximum eccentricity), isostatic changes and movements of sea-level as causing rhythmic arrangement of strata. No described case appears to explain the Shoalhaven series.

The light bands are little—if at all—coarser than the dark, precluding the explanation of seasonal rapid transport of sandy sediments caused by heavy rainfall on land and slow, subsequent deposition of finer particles. Nor does it fit in with Barrell's Slatedale case; especially as only the light and dark bands are represented—sometimes nearly equal in thickness—and beds which should have been formed of a mixture of the two during periods of quiet between storms, do not occur; see Barrell (1917, p. 803) as already quoted: "the ribbons often consist of a band of soft black mud-rock overlain by a band of nearly clean sand. The mixture of the two would appear to give the normal composition shown in the intervening beds."

The essential similarity in composition of the light and dark bands (except, mainly the higher percentage of carbonaceous material) suggests that both were formed of the same sediment, but at greatly different rates. The light bands would possibly represent slow deposition with oxidation of organic content, the dark, periods of rapid deposition with sudden entombment of pelagic, planktonic organisms. Showering of volcanic ash on the sea would fit the facts and agree with the findings of Joplin (1946, pp. 167, 170).

The planktonic fauna and flora may have been killed and carried to the bottom by the initial heavy falls of fine ash when eruptions began, exhausting the supply of organic material so that following falls were practically free from it. Formation of the sharp upper margins of the dark bands postulates a break between the initial and following eruptions. Again, the time between falls could not have been long enough to permit the building up of planktonic material by immigration or natural increase; otherwise the margins would be blurred and the upper layers dark with organic matter instead of light.

There appears to be no possibility that seasonal fluctuations could have caused the necessary sharp alternation in the size of the floating population of the sea.

An explanation might be that each heavy fall of ash laid down a homogeneous layer of sediment. In the quiet sea, movement was reduced to a minimum and oxidation affected only the upper part of the layer, forming a paired band—a light coloured layer overlying an untouched lower layer dark with organic material. Each considerable fall of fine volcanic ash, occasionally mixed with small crystals and mineral fragments, would repeat the process and be represented by a paired band unless the fall followed too closely on the preceding one. This explanation appears to be precluded by the sharp demarcation between the bands.

The same reason militates against the chance that the light bands were composed of rhyolitic ash and the dark from more basic sources. Also, there would have needed to be an unlikely regularity in alternation of eruptions or, if both sets of volcanoes were in eruption simultaneously, a fortuitous geographical arrangement of the acid and more basic vents combined with extreme regularity in seasonal changes of wind such as, for example, the north-west monsoon and south-east Trades in Torres Strait.

### III. SUMMARY.

A rhythmical sequence of 657 bands of phyllite arranged regularly in alternate light and dark coloured layers is described. The presence or absence of carbonaceous material is held to control the colours of the contrasted bands. It is suggested that rapid deposition of volcanic ash, which killed and entombed the plankton, formed the dark bands. The light bands formed during periods of volcanic quiescence when oxidation was not impeded. Extremely slow deposition would be expected to eliminate carbonaceous material. Thicknesses of the light bands would be proportional to the length of time between periods of volcanic activity, and the thicknesses of the dark would be proportional to the intensity of volcanic activity.

### IV. ACKNOWLEDGEMENTS.

I wish to thank Professor L. A. Cotton for suggesting the presentation of this paper and also for advice, Dr. J. A. Dulhunty for making a chemical analysis, and Dr. W. R. Browne and Dr. G. A. Joplin for examining rock sections. Dr. Browne also kindly read the manuscript and made corrections and suggestions.



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## EXPLANATION OF PLATE V.

Fig. 1.—Bands approximately in the middle section of the lower phase of the series (Phase I).

Fig. 2.—Bands in the upper phase of the series (Phase III), showing practically identical characters with those of Phase I; the two end phases are separated by the irregular Phase II which reflects more unsettled conditions.

Author's photographs.

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## CATALOGUE OF REPTILES IN THE MACLEAY MUSEUM.

## PART II. SPHENOMORPHUS SPALDINGI (MACLEAY).

By STEPHEN J. COPLAND, B.Sc.

(Plate iv; three Text-figures.)

[Read 29th May, 1946.]

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## I. INTRODUCTION.

This second paper on the reptiles in the Macleay Museum at the University of Sydney deals with another of William Macleay's types—*Sphenomorphus spaldingi*. Like the two species dealt with in the preceding paper—*Sphenomorphus pardalis* and *S. nigricaudis*, *S. spaldingi* has undergone vicissitudes because of its original scanty description. From the issue of the third volume of Boulenger's Catalogue in 1887 until recently it has been consistently identified as *Lygosoma dorsale* Boulenger. A redescription of a lectotype selected from the four cotypes, variation of the three specimens which now become paratypes, comparisons with Queensland, Northern Territory and Torres Strait specimens in the Australian and Queensland Museums, distribution, and notes on *Lygosoma dorsale* are included here.

## II. ORIGINAL DESCRIPTION AND REDESCRIPTION OF COTYPES OF SPHENOMORPHUS SPALDINGI.

Of the four cotypes (MR 418–421) labelled "*Lygosoma (Hinulia) spaldingi* Macleay. Endeavour River" in the Macleay Museum at the University of Sydney, the largest, MR 419, has been designated the lectotype; the remaining three specimens then become paratypes.

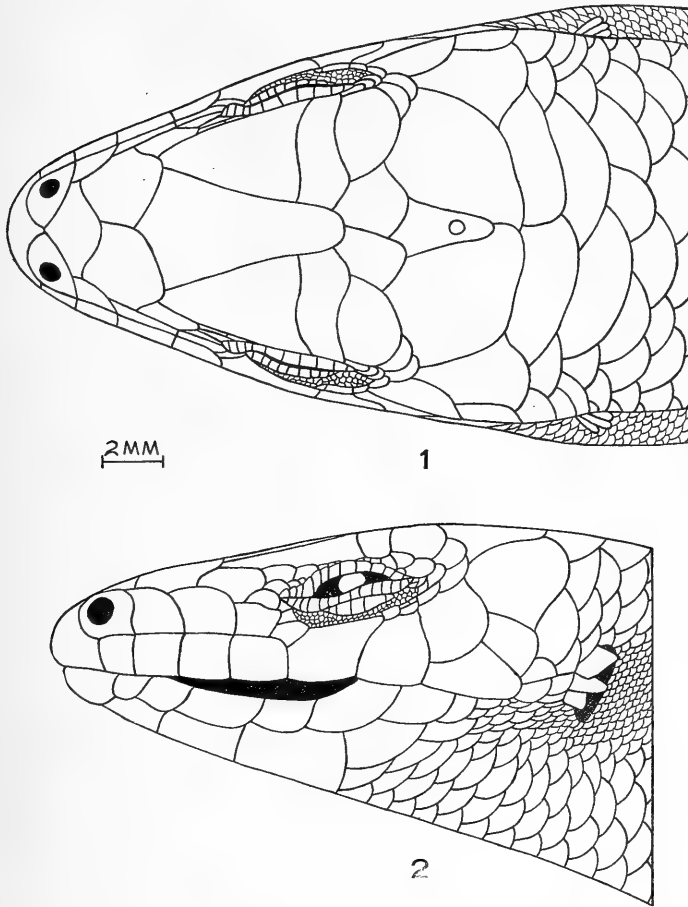
Macleay's original description (1877, p. 63) is now given, followed by an extended, standard redescription of the lectotype.

"Ear opening moderate and oval, with three large denticulations in front; nasal, rostral, and internasal plates touching, or nearly so, at an acute point; frontonasals contiguous for some distance; supraoculars three on each side, the anterior plate very large and triangular, its apex touching the frontonasal; scales on the back in four series; legs rather slender; hind toes elongate; two large preanal scales; tail very fine and tapering; colour, above pale olive brown, with three broad longitudinal black white-edged stripes, one vertebral, the others lateral and marked with a line of large white patches; the under surface is white, with black spots on the sides and labial plates; the legs are light-coloured with black stripes.

"A number of this species were obtained from the Endeavour River. Like many of the genus it seems to vary much. Two of the specimens before me are without the vertebral black stripe, and the nasal plates are not contiguous."

*Description of Lectotype.*—Rostral moderately high, the area visible from above slightly less than that of the frontonasal; long, concave sutures with nasals, and nearly straight, vertical ones, a third the length of those with the nasals, with 1st supralabials;

the suture with the frontonasal is so short that it barely separates the nasals. Nasals large; roughly oval nostrils, half the length of the scale, slightly in front of the midline; sutures long and convex with rostral and frontonasal; sinuous, but nearly straight, with anterior loreal; and straight with the entire upper margin of 1st supralabial. Frontonasal moderate in size, about equal to a nasal, smaller than a prefrontal, and about a third the area of the frontal, from which it is separated by at least two-thirds its own length; long, concave sutures with nasals, nearly straight ones the same length with prefrontals, and very short ones with anterior loreals. Prefrontals large, roughly hexagonal, in contact with each other, the long suture equalling half the greatest length of the scale; other sutures, long and about equal in length with frontonasal and frontal,



Figs. 1 and 2.—Head of *Sphenomorphus spaldingi*. 1. Dorsal view. 2. Lateral view.

considerably shorter with each loreal and 1st supraciliary, quite short with 1st supraocular. Frontal large, kite-shaped, twice as long as broad, considerably longer than frontoparietals and interparietal together, long, straight, postero-lateral sides against 1st supraoculars for about three-quarters their length, remainder against 2nd supraoculars and frontoparietals, widely separated from 3rd supraoculars; posterior end rounded; antero-lateral sutures with prefrontals. Frontoparietals considerably smaller than prefrontals, each in contact with its fellow, frontal, 2nd and 3rd supraoculars, parietal and interparietal. Interparietal kite-shaped, small, half the length of the frontal, enclosed between parietals and frontoparietals; rounded pineal area at junction of middle and posterior thirds. Parietals are the largest head shields, the area of each being slightly more than that of the frontal, compact but irregular in shape, long postero-

lateral border in contact with a nuchal (right scale narrowly touching second member of 1st pair), and upper secondary temporal; antero-lateral border against 3rd supraocular and narrowly with 15th supraciliary and 2nd postocular, antero-medial with frontoparietal; separated by interparietal except for short suture one-third the length of the interparietal. There are two, well-differentiated pairs of nuchals. Seven supralabials, 5th much the largest and bounding the eye ventrally, there being no suboculars; 6th capped by two, narrow, flattened postsuboculars and completing the lower margin of the eye; 1st to 5th scales roughly oblong, 6th and 7th pentagonal, each with prominent point dorsad; size in decreasing order, 5, 6, 7, 3, 4, 2, 1; 7th supralabial separated from ear by four scales, two above two. Primary temporal large, squarish, posteriorly against secondary temporals, ventrally between 6th and 7th supralabials, anteriorly in contact with 2nd and 3rd postoculars and a postsubocular. Upper secondary temporal twice size of lower, which is a little smaller than the primary temporal; between parietal, anterior nuchal, body scale, tertiary temporal, lower secondary temporal, primary temporal, and 2nd postocular. Lower secondary temporal between other three temporals, 7th supralabial and one of two small scales separating it from the ear. Tertiary temporal elongated vertically, separated from ear by one or two scales. Body scales begin behind the nuchals, secondary temporals and tertiary temporal. The loreals are large, the anterior taller than broad and the posterior broader than tall; the anterior lies exactly against the whole of the upper margin of the 2nd supralabial and the posterior exactly against the whole of the upper margin of the 3rd supralabial; besides the anterior loreal and 3rd supralabial the posterior loreal is in contact with the prefrontal, 1st supraciliary and lower preocular. Upper and lower palpebral series abut against the upper preocular, which is also in contact with 1st supraciliary, upper accessory palpebral (wedged between the palpebral chain and 2nd supraciliary), lower preocular and small scales forming part of the lower eyelid. The lower preocular is twice the size of the upper and lies between it, 1st supraciliary, posterior loreal, 4th supralabial, presubocular and small scales of the lower eyelid. The presubocular is wedged between the lower preocular, 4th and 5th supralabials and above joins the small scales of the lower eyelid. The postoculars are three small scales; the 1st small and anteriorly in contact with the 14th and 15th supraciliaries, and small scales of the lower eyelid, posteriorly against the 2nd and 3rd postoculars; the 2nd is much the largest scale and in addition to both other postoculars is in contact with the 15th supraciliary, parietal, upper secondary temporal and primary temporal; the 3rd lies in front of the primary temporal. The upper palpebral series consists of about 12 small, but stout, scales, the lower palpebral series of about 15. The lower eyelid has a large, transparent, scaly plate and then passes into a great number of tiny scales which abut on preoculars, presubocular, 5th supralabial, postsuboculars, 2nd and 3rd postoculars and 14th supraciliary. There are 15 supraciliaries, but only the anterior three and the posterior three are of any size, the remaining nine being very small and forming the margin of the upper eyelid; the 1st is by far the largest, the 15th, 2nd, 14th and 13th, in that order, ranking next; the 1st is rather widely separated from the frontal and lies between prefrontal, 1st supraocular, 2nd supraciliary, upper accessory palpebral, preoculars and posterior loreal; the 13th, 14th and 15th are all in contact with the 3rd supraocular, the 13th also with the 2nd; the 14th and 15th are nearly separated by the 1st postocular; the upper and lower palpebral series end against the 14th. There are three large supraoculars, the 1st being slightly larger than the other two combined; the triangular 1st lies between prefrontal, frontal, 2nd supraocular, and 1st to 10th of the supraciliaries; the 2nd is a band twice as wide as long, extending between the other two supraoculars from the 10th to 13th supraciliaries to the frontal and frontoparietal; the triangular 3rd lies between the 13th to 15th supraciliaries, 2nd supraocular, frontoparietal and parietal. Six infralabials (a small, single scale only on the left might possibly be added), 1st scale much the smallest, and 5th the largest. Medium sized mental in contact with nearly half the lower border of the 1st supralabial when the mouth is closed. The large, broad postmental is in contact with at least two-thirds of the lower margin of the 2nd infralabial and the whole of the lower margin of the 1st on each side, the anterior chin-shields and mental, making seven shields in all. Three large pairs of chin-shields;

1st slightly larger than 2nd, which is considerably larger than 3rd; 1st pair in contact, 2nd separated by a single, fairly large scale, and the 3rd by three small scales, only the central one of which differs from the succeeding body scales.

Ear opening oval, greater diameter subequal to length of eye; with three, large, triangular denticulations occupying the whole of the anterior margin, the dorsal scale is the largest, the ventral the smallest, and the intermediate one has a prominent median keel.

Scales in 32 rows at midbody, dorsal scales considerably larger than ventral, lateral scales much smaller again. Caudal scales dorsally practically maintain their size to near the tip of the tail, but decrease in number; lateral caudal scales larger than the dorsal; one median row of transverse ventral scales, beginning about six scales behind the vent, very large, and towards the end of the tail extending up the sides. Two large preanal scales, each at least twice the size of an adjacent body scale. Scales from above vent to parietals, 57. Habitus compact, the body only slightly depressed. Snout about equal in length to the distance between the eye and ear. The distance between the snout and forelimb is contained 1.77 times in the distance between axilla and groin. Tail tapering gradually from body size to a very fine point, which is slightly frayed but apparently not abbreviated; nearly twice the length of head and body. Limbs moderately long and powerful, hindlimb overlapping forelimb, when adpressed, to between wrist and elbow. Fingers and toes compressed. Length of fingers in decreasing order, 3, 4, 2, 5, 1; of the toes, 4, 3, 2, 5, 1. Lamellar formula for fingers, 8, 11, 13, 14, 9. There is a large number of small rounded scales on the palm, surrounded by large scales at the sides (where they extend back from the 1st and 5th fingers) and wrist. Lamellar formula for toes, 9, 13, 16, 24, 13. Insertion of the 5th toe is nearly its own length from that of the 4th; large scales running back from the 4th, 5th and 1st toes, and margining the heel, enclose the sole consisting of a large number of small rounded scales.

Measurements of the lectotype are given with those of the paratypes.

Colour: Dorsal surface of head and body is pale brown. A dark brown vertebral stripe one scale wide (two half scales) runs between the limbs, anteriorly tapering to a fine point between the nuchals and against right parietal, and dying out about 14 scales behind the hindlimbs. The vertebral stripe is margined on each side by a white line about a fifth of a scale wide. Two similar white dorso-lateral lines run from the outer edges of the nuchals to more than two-thirds the length of the tail, becoming gradually less distinct posteriorly. On each side the dorso-lateral white line margins a brown band, generally between half and one scale wide. From just in front of the forelimbs to just behind the hindlimbs this band sends down to half the depth of the sides about 18 irregular, hour-glass-shaped blotches. The band, lacking the ventrally-directed blotches, continues rather irregularly for the proximal three-quarters of the tail. Along the lower half of each side run two most irregular, ill-defined, disconnected lines of brown blotches ventral to the main brown band. The lower of the two tends to form a stripe low down on each side of the tail to as far as the distal fourth. There are about half a dozen dark brown dots on the posterior half of the head. Laterally the posterior loreal, temporals, supralabials and infralabials are splotched. There are three rough longitudinal stripes dorsally and laterally along each forelimb, and four along the hindlimbs. Head, body, limbs and tail are ventrally whitish to very pale brown.

*Variation in Paratypes* (MR 418, MR 420-1).—The rostral which just touches the frontonasal in MR 419 has contacts varying between one-sixth and one-quarter the width of the frontonasal in the paratypes. Nasals are also in contact with the 2nd supralabial—to at least a third its length in MR 418 and MR 420. The frontonasal in MR 420 and MR 421 is at least equal in area to a prefrontal; it is separated from the frontal by about a third its own length in MR 420 and by less than half in MR 421. Length of the contact between the prefrontals in all three specimens is less than in MR 419, being least in MR 420 where it is only a quarter or less of the greatest length of a prefrontal. In MR 421 the caudal third of the frontal is divided off by a transverse suture. There are three pairs of nuchals in MR 420 and MR 421, three on the left and four on the right in MR 418. Three small scales separate the ear from the last supralabial in each paratype. In MR 418 an additional supralabial is interpolated before the subocular scale on the left

side; this condition is found on each side in MR 420. Contacts of the loreals with the supralabials vary slightly. The presubocular is larger in the paratypes than in the lectotype. The scaly lower eyelid appears to be transparent in all specimens. Number of supraciliaries is 12 or 13. Proportions and relationships of the three supraoculars agree strictly with those of the lectotype. The middle denticulation is the largest on the anterior margin of the left ear in MR 421. There is a very small fourth ventral denticulation on each side in MR 420, and on the left side the dorsal one is scarcely larger. Scales are in 28 rows at midbody in MR 418 and MR 420, 30 in MR 421. The series of wide subcaudals starts about three scales behind the vent in MR 421, four in MR 418, and five in MR 420. There are 59 scales from above the vent to the parietals in MR 418, 58 in MR 420, and 65 in MR 421. Lengths of the limbs in MR 418 resemble those of the lectotype; when adpressed, the hindlimb of MR 420 reaches to the shoulder, and that of MR 421 to between the elbow and the shoulder.

*Lamellar Formulae for Fingers and Toes.*

	Fingers.					Toes.				
	1	2	3	4	5	1	2	3	4	5
MR 418 .. ..	6	10	14	14	9	7	11	18	23	11
MR 419 .. ..	8	11	13	14	9	9	13	16	24	13
MR 420 .. ..	6	9	14	15	8	7	12	19	24	11
MR 421 .. ..	7	11	12	12	8	8	13	19	23	12

*Measurements of Lectotype and Paratypes of Sphenomorphus spaldingi in mm.*

	MR 418	MR 419	MR 420	MR 421
Snout-vent .. ..	73	97	66	74
Tail .. ..	158	183	149	146
Snout-forelimb .. ..	24	30	23	23
Axilla-groin .. ..	42	53	33	39
Head, length* .. ..	14	17	13	13
Head, width .. ..	9	12	8.5	9
Forelimb, length .. ..	17	25	18	20
Hindlimb, length .. ..	31	40	32	34
Width of body .. ..	11	c. 14	10	10

\* Length of the head is measured from the tip of the snout to the suture between parietals and nuchals.

The dorsal ground colour of head and body in the three paratypes agrees fairly closely with that of the lectotype, although the brown is a little deeper in MR 421 and more greenish in MR 420. In all four the tails are deeper brown than the body. The prominent dark brown, almost black, vertebral stripe of MR 419 is missing in MR 418 except for a most inconspicuous trace between the neck and forelimbs; in MR 420 it is narrow and much less prominent than in MR 419, but runs the same length; in MR 421 it is reasonably noticeable in front of the forelimbs but then becomes reduced to a thin zigzag line margining the extreme median borders of the two rows of mid-dorsal scales. The well-marked white lines on each side of the vertebral stripe in MR 419 are missing in MR 418 and only noticeable to near the hindlimbs in MR 420 and not even as far as the forelimbs in MR 421. The white dorso-lateral lines are prominent in all four specimens. The brown band ventral to each dorso-lateral white line varies somewhat but remains characteristic. In MR 421 it is especially well-marked with about 24 hour-glass-shaped blotches. It is less conspicuous in the other two paratypes, where it does not continue along the sides of the tail. All four lizards have a white lateral stripe, below which the ill-defined brown blotches of MR 419 are represented by an almost continuous stripe in MR 421, and faint stripes, hardly amounting to more than discolorations, in MR 418 and MR 420. Brown dots are missing on the posterior half of the head in MR 418 and MR 421, but represented by four smudges in MR 420. All heads are laterally spotted or smudged with brown. Stripes along the limbs vary in intensity,

but all tend to resemble the pattern of the lectotype. All ventral surfaces are whitish except those of the tails, which are very pale brown.

III. LOCALITY RECORDS AND SPECIMENS EXAMINED.

*Specimens examined and Locality Records of Sphenomorphus spaldingi.*

- 4 (MR 418—21, Macleay Mus.) Endeavour River, Qd., no date, lectotype and paratypes.
- 1 (R 2262, Aust. Mus.) Bloomfield River, nr. Cooktown, Qd. (George Hislop), 2.xii.1897.
- 3 (R 3495-7, Aust. Mus.) Mapoon, Gulf of Carpentaria, Qd., no date.
- 1 (R 3958, Aust. Mus.) Cooktown, Qd. (E. A. Olive), March, 1908.
- 1 (R 4539, Aust. Mus.) Somerset, Cape York, Qd. (Hedley and McCulloch), June, 1909.
- 1 (R 6372, Aust. Mus.) no data.
- 2 (R 9654-5, Aust. Mus.) Badu Island, Torres Strait (Melbourne Ward), 14.xi.1928.
- 2 (R 12387, Aust. Mus.)\* Yirrkala, N.T. (Rev. W. S. Chaseling), 21.viii.1939.
- 2 (—, Aust. Mus.)† Yirrkala, N.T., no date.
- 2 (J1698-9, Qd. Mus.) Cape York, Qd., no date.

Qd., Queensland; N.T., Northern Territory.

\* Described as R 12387A and R 12387B.

† Described as C and D.

A note in the Australian Museum register records that R 3957, collected with R 3958, was sent to T. Barbour.

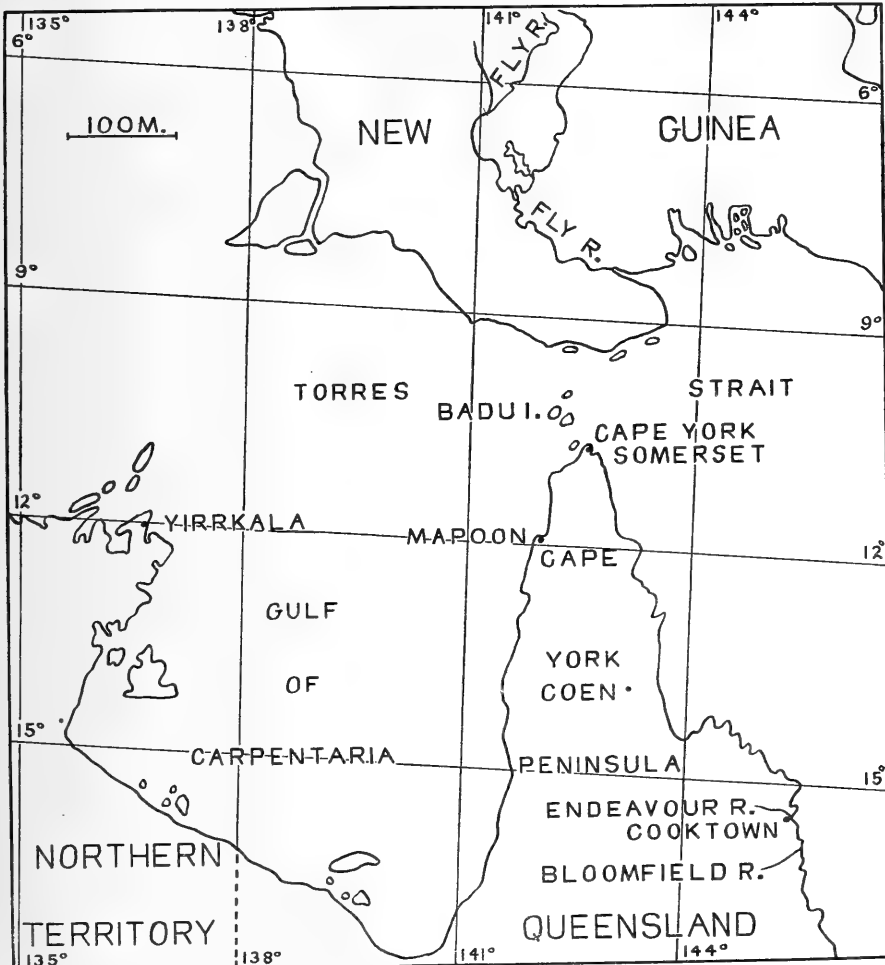


Fig. 3.—Map showing all locality records of specimens.

The two specimens (J 1698-9) from the Queensland Museum were forwarded by the director, Mr. George Mack, with the note: "They are the pick of six examples in the collection, all of which have the general locality of Cape York, Queensland, and lack other particulars."

*Variation in Specimens from the Australian and Queensland Museums.*—Localities may be identified in the text by the following letters in brackets placed after the number: E, Endeavour River; B, Bloomfield River; M, Mapoon; C, Cooktown; S, Somerset; I, Badu Island; Y, Yirrkala; K, Cape York. R 6372, whose locality is not known, is marked (?).

In all specimens the area of the rostral visible from above is a little more than half that of the frontonasal. In R 12387A (Y), R 12387B (Y), C (Y), D (Y), R 6372 (?), and J 1699 (K) the suture of the rostral with the frontonasal is wider than in the type, but still narrow, in the remainder the suture is considerably wider again. The nasals are almost invariable in shape, but a few are not in contact with the entire upper margin of the 1st supralabial. This is most marked in three of the four Yirrkala specimens, but D is normal. Again in R 3495 (M) and R 9654 (I) the nasal touches the 1st supralabial. Size of the frontonasal to that of the frontal varies between slightly less than  $\frac{1}{2}$  and  $\frac{3}{4}$ . In two Yirrkala specimens the frontonasal is narrowly in contact with the frontal, in the other 13 cases separation to the length of the frontonasal varies between  $\frac{1}{2}$  to  $\frac{3}{4}$  (1,  $\frac{1}{2}$ ; 5,  $\frac{1}{2}$ ; 2,  $\frac{3}{4}$ ; 1,  $\frac{3}{4}$ ; 4,  $\frac{3}{4}$ ). Prefrontals are very constant, any variation being caused by the frontonasal-frontal relationship just dealt with. The frontal is sometimes quite slender, and considerably more than twice as long as wide in R 3958 (C), R 4539 (S), R 9654 (I), and J 1698 (K); as much as 80 per cent. of the postero-lateral border may be in contact with the 1st supraocular. Frontoparietals occasionally approach the prefrontals in size. The interparietal may be somewhat squat or considerably elongated. It is sometimes less than half the length of the frontal; and abnormal and short in R 9654 (I). Length of the suture between the parietals to the length of the interparietal varies between a quarter and a half. Nuchals are rather variable: J 1698 (K) has two pairs, J 1699 (K) and R 3958 (C) two pairs and a large unpaired scale on the right, R 2262 (B) and R 6372 (?) two pairs and one on the left, R 12387A (Y) and D (Y) three pairs, R 3497 (M), R 9654 (I) and R 9655 (I) three pairs and one right, R 3495 (M), R 4539 (S) and C (Y) three pairs and one left, and R 3496 (M) and R 12387B (Y) four pairs. The 7th supralabial may be separated from the ear by a cluster of small scales, three or four in line. There are eight supralabials in R 2262 (B) and R 12387A (Y), an extra scale being interpolated before the normal 5th. In R 2262 (B) the upper secondary temporal is very large and includes much of the lower secondary temporal, which is exceptionally small. There is a tendency for the body scale behind the tertiary temporal to become enlarged, forming with the temporal two nearly identical, vertically-elongated scales. The posterior loreal is in contact with the upper preocular in two Mapoon specimens. Sutures between and behind the loreals frequently do not correspond with those between the 2nd and 3rd and 3rd and 4th supralabials, this being, of course, especially noticeable in individuals with eight supralabials. The upper preocular as in R 12387A (Y) may practically equal the lower in size. In R 3958 (C) the upper is in contact with the 2nd supraciliary as well as the upper accessory palpebral. In R 6372 (?) the lower is separated from the presubocular by the small scales forming part of the lower eyelid. Three specimens have the dorsal third of the presubocular divided off to form a separate scale. The postoculars—although small—are remarkably constant in maintaining their relationships with the posterior two supraciliaries and the other surrounding scales. Supraciliaries number 11 (3 times), 12 (5), and 13 (7). The three supraoculars on each side in all specimens are most regularly arranged. R 9654 (I) has seven infralabials. R 2262 (B) has the postmental narrowly in contact with the 3rd infralabial as well as the 1st and 2nd. The median denticulation of the ear may be the largest. J 1699 (K) has only two denticulations on the left side; R 3497 (M) and R 9654 (I) four on each side; R 12387A (Y) and R 12387B (Y) four on the right and five on the left; and C (Y) and D (Y) four on the left and five on the right. Midbody scale rows vary between 26 and 32: 26; J 1699 (K): 28; J 1698 (K), R 3495-7 (M), R 3958 (C), R 9655 (I), R 12387B (Y), C (Y) and D (Y): 30; R 4539 (S), R 6372 (?), R 9654 (I) and R 12387A (Y): 32; R 2262 (B). The large subcaudal scales begin from two to six scales behind the



vent; most commonly three; 2, 4, 5, and 6 being each only represented by one specimen. Number of scales from above vent to parietals varies between 54 and 64 (1, 54; 2, 55; 1, 57; 1, 59; 3, 60; 1, 61; 3, 62; 2, 63; 1, 64). The hindlimb reaches to various points between the wrist and the axil when the limbs are adpressed, the limbs being proportionately longer in young individuals. Number of lamellae under the 4th toe varies between 21 and 26 (3, 21; 6, 22; 1, 23; 2, 24; 2, 25; 1, 26) and appear to have little geographical significance.

*Measurements in mm. of Specimens of Sphenomorphus spaldingi in the Australian and Queensland Museums.*

Number.	Snout-Vent.	Tail.	Snout-Forelimb.	Axilla-Groin.	Head.		Length.		Width of Body.
					Length.	Width.	Forelimb.	Hindlimb.	
R 2262 (B) ..	98	203	32	53	18	14	22	42	16
R 3495 (M)	77	125	24	46	13	10	17	31	13
R 3496 (M)	60	128	20	30	11	8	14	27	9
R 3497 (M)	49	106	17	26	10	7	13	23	8
R 3958 (C) ..	49	23 +	17	23	11	7	14	24	7
R 4539 (S)	38	78	15	19	9	5-5	11	19	6
R 6372 (?) ..	114	90 +	33	64	20	15	26	43	21
R 9654 (I) ..	96	150 +	30	54	17	11	22	42	14
R 9655 (I) ..	90	139	26	52	16	10	20	37	13
R 12387A (Y)	83	170	15	48	16	11	20	34	14
R 12387B (Y)	81	182	14	43	14	10	18	33	13
C (Y) ..	94	172	30	49	16	11	24	42	13
D (Y) ..	60	100	20	30	12	8	16	40	9
J 1698 (K) ..	67	125	24	36	13	9	17	31	9
J 1699 (K) ..	71	158	14	37	14	9	17	33	10

*Variation in Colour.*—The dorsal ground colour shows variation in shades of brown, some individuals being deep brown, others light tan, and a few with a suggestion of green or grey. The blackish vertebral stripe resembles that of the lectotype in R 2262 (B), R 6372 (?), C (Y) and R 12387A (Y); it is thinner and less pronounced in R 9655 (I), D (Y) and R 12387B (Y); almost obsolete in R 3496 (M), R 3497 (M), R 3958 (C), R 4539 (S) and R 9654 (I); a merest trace in R 3495 (M) and J 1699 (K); and absent in J 1698 (K). The white lines edging the blackish vertebral stripe are typical in R 2262 (B), R 6372 (?) and R 9655 (I); poorly developed in C (Y), D (Y), R 4539 (S) and R 9654 (I); merest traces in R 3496 (M), R 3497 (M), R 12387A (Y) and R 12387B (Y); and absent in R 3495 (M), R 3958 (C), J 1698 (K) and J 1699 (K). The white dorso-lateral lines and the blackish or blackish-brown longitudinal bands below them are fairly typical (the hour-glass-shaped blotches varying in number between 20 and 24), except in the four Yirrkala specimens where wide stripes form a mosaic of white and black with suggestions of three or four interrupted dark lines and two white ones. The dorsal and ventral elements of the blackish band may form two distinct lines along the proximal two-thirds of the tail before merging. It may then run practically to the tip of the tail. Unlike the lectotype, but resembling the paratypes, 14 specimens have a distinct black line running the length of the body on the median margin of the white dorso-lateral line. The ill-defined ventro-lateral blotches of the type series (except MR 421) are represented by reasonably well-marked vertical bars in R 2262 (B), but in the remaining specimens are either missing or reduced to a more or less ill-defined line or longitudinal series of brown smudges. Heads are blotched laterally and dorsally to varying extents, the markings being sometimes confined to the temporals and supralabials.

#### IV. LYGOSOMA DORSALE BOULENGER AND REFERENCES IN LITERATURE.

Boulenger (1887, p. 226) described *Lygosoma dorsale* from the Fly River, New Guinea. From his description, which follows, and figure on Plate xii, it is certain that *Lygosoma dorsale* is identical with *Sphenomorphus spaldingi*.

"Closely allied to *L. lesueurii*. Only three supraoculars, first very large; frontal much longer than frontoparietals and interparietal together. Two or three auricular

lobules. Adpressed limbs slightly overlapping. Thirty scales round the body. Pale brown above; a black vertebral streak; a yellowish, black-edged lateral streak; a lateral series of black spots and an ill-defined light, dark-edged streak from axilla to groin; lower surfaces white. From snout to vent 94 mm., head 20 mm., width of head 11 mm., forelimb 22 mm., hindlimb 39 mm. New Guinea. *a-b*, adult, Fly River. Rev. S. Macfarlane (C.)."

Zietz (1920, p. 206) notes that *Lygosoma dorsale* and *Hinulia spaldingi* are synonymous, and at the same time lumps the *taeniolata-essingtonii-maculata-lesueurii* (= *australis*)-*inornata-dorsale-spaldingi-leae-fischeri-strauchii* group under *Lygosoma taeniolatum*, and gives the range as all mainland States and New Guinea.

This lumping was challenged by Loveridge (1934, p. 347): "The action of Zietz in synonymizing half a dozen species with this name is quite unjustifiable. Nor can they be regarded as races if that was his intention."

Similarly Waite (1929, p. 149) reproduces Boulenger's figure of *Lygosoma dorsale* (1887, Plate xii) under the heading of *Hinulia taeniolata*, a species to which it bears little resemblance.

De Rooij (1915, p. 175) closely follows Boulenger's description, but adds the following details: scales round the body 28 as well as 30, length of tail 130 mm. (the head and body length being 94 mm. as given by Boulenger); habitat; islands of Torres Strait, near Cooktown, and the Fly River.

Loveridge (1934, p. 346) synonymizes *Lygosoma dorsale* with *Hinulia spaldingi*, and gives notes on six specimens in the Museum of Comparative Zoölogy at Harvard College (M.C.Z. 35374-9) collected at Coen in 1932 by P. J. Darlington: "midbody scale rows 26-28; supraoculars 3; prefrontals broadly, or narrowly, in contact, or well separated. Largest skink (No. 35374) measures 312 (99 + 213) mm."

#### V. ACKNOWLEDGEMENTS.

I wish to thank Professor W. J. Dakin and Professor E. A. Briggs, of the University of Sydney, and Dr. A. B. Walkom and Mr. J. R. Kinghorn, of the Australian Museum, for advice and assistance. Mr. Kinghorn and Mr. G. Mack, of the Queensland Museum, kindly lent me specimens. Mr. J. Henry, Curator of the Macleay Museum, co-operated by making available specimens in his charge. I also have to thank Miss A. G. Burns, of the University of Sydney, for the photographs.

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#### EXPLANATION OF PLATE IV.

- Fig. 1.—Dorsal view of lectotype of *Sphenomorphus spaldingi* (MR 419).
- Fig. 2.—Dorsal view of paratype of *Sphenomorphus spaldingi* (MR 418).
- Fig. 3.—Lateral view (slightly tilted dorsally) of MR 418.
- Fig. 4.—Dorsal view of *Lygosoma dorsale*, from Boulenger (1887, Plate xii).
- Lengths of head and body of MR 419, MR 418 and Boulenger's specimen are 97, 73 and 94 mm. respectively.
- [Photos of MR 419 and MR 418—Miss A. G. Burns.]

CONTRIBUTIONS TO THE GEOLOGY OF HOUTMAN'S ABROLHOS,  
WESTERN AUSTRALIA.\*

By CURT TEICHERT, D.Sc.

(Communicated by Dr. W. R. Browne.)

(Plates vi-xvi; seven Text-figures.)

[Read 31st July, 1946.]

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SITUATION, DISCOVERY AND NAME.

Houtman's Abrolhos, situated between  $28^{\circ} 15\frac{1}{2}'$  and  $29^{\circ} 00\frac{1}{2}'$  S. Lat., approximately 40 miles off the coast of Western Australia, are the southernmost coral islands in the Indian Ocean. They were discovered by the Dutchman Frederik Houtman in 1617, though they were not named in print until 1627, when they are shown on Hessel Gerritszoon's first map as "Fr. Houtmans abrolhos" ("Caert van 't Land van d'Eendracht, A<sup>o</sup> 1627", reproduced by Heeres, 1899, pp. 8-9). On another map published by Hessel Gerritszoon in 1628 the islands appear as "Houtmans Abrolhos", a version which has since been preserved by most travellers and authors. The islands are called "Houtman Rocks" on all British Admiralty charts, but there seems little justification

\* The publication of this paper has been made possible by a grant from the Commonwealth Scientific Publications Committee.

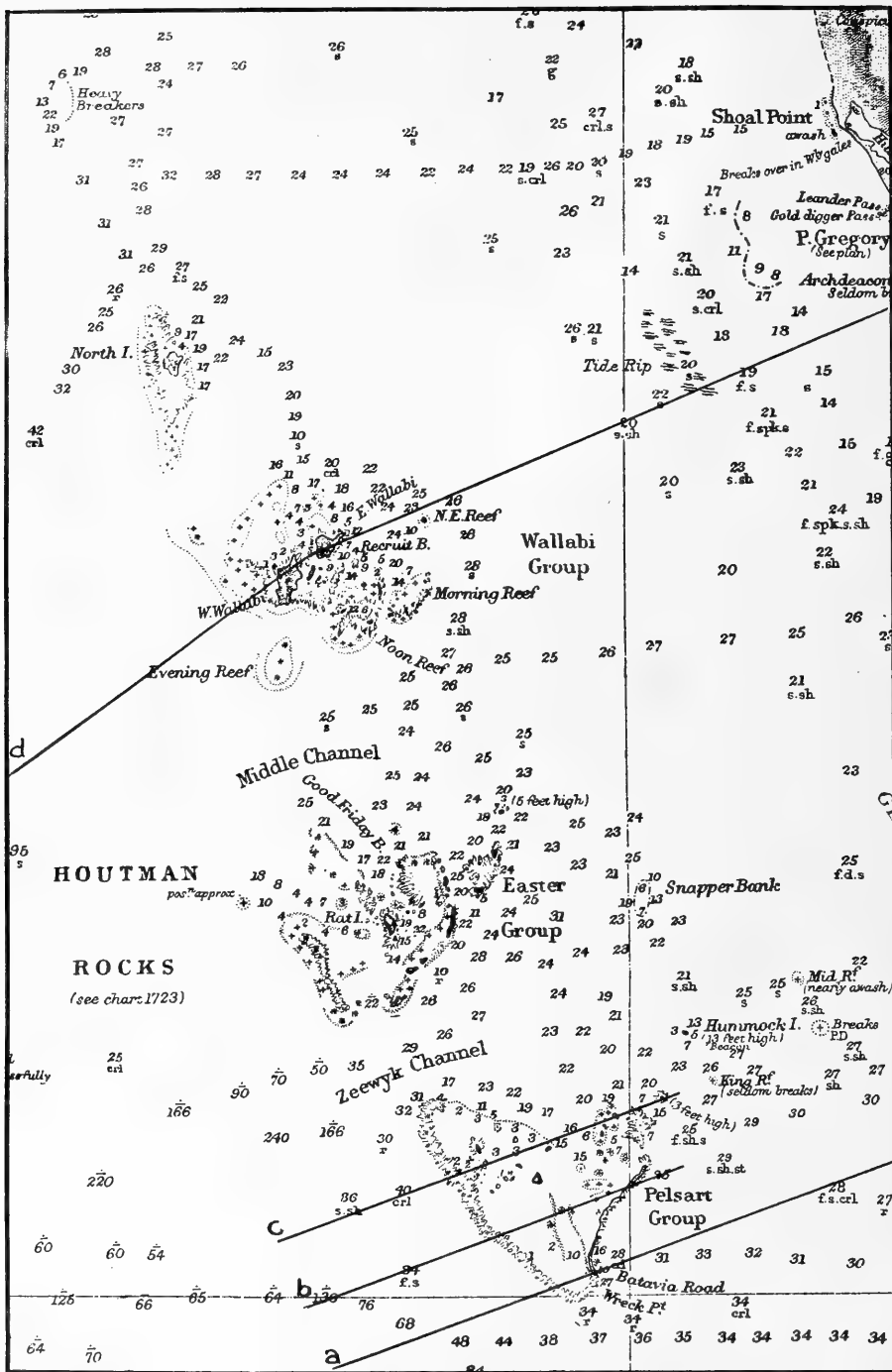


Fig. 1.—Map of Houtman's Abrolhos. Scale about 1 inch = 8 nautical miles. (Reproduction from British Admiralty Chart 1056, with additions. *a-c*, Sections through the Pelsart Group, see Fig. 6; *d*, Section through Wallaby Group, see Fig. 7.

for such a change of name. In Western Australia the islands are generally known as the "Abrolhos Islands", or simply "The Abrolhos". According to Battye (1924) the name is a contraction from the Portuguese *Abri vossos olhos*, meaning "keep your eyes open"—an obvious reference to the great danger which these low-lying islands present to navigation along this part of the coast. To this day they carry no lighthouse.

#### GENERAL DESCRIPTION.

Houtman's Albrolos are not, as has sometimes been stated, the most southerly situated coral islands of the world. Lord Howe Island, in the Tasman Sea, situated at  $31\frac{1}{2}^{\circ}$  S. Lat., has a fringing reef along its west coast, and the Middleton and Elizabeth reefs, between  $29^{\circ}$  and  $30^{\circ}$  S. Lat., also in the Tasman Sea, are, according to Davis (1928), small bank atolls. Houtman's Abrolhos are, however, the southernmost coral islands of the Indian Ocean.

They are geographically somewhat isolated, for the nearest coral reefs in Western Australia are found 150 miles to the north, along the west coast of Dirk Hartog Island (Hartmeyer, 1907, p. 90).\*

The Abrolhos Group consists of four rather well distinguished geographical units. The northernmost of these is *North Island*, an island about a square mile in area which is surrounded by a tidal flat on all sides and bordered by a fringing reef on the western side. To the south-east follows the *Wallaby Group*, comprising a number of islands of various sizes, banks, and reefs of rather irregular shape.

The two largest islands, East and West Wallaby, rise from a limestone platform situated at or slightly below low-water level. This limestone platform is bordered to the west by arcs of fringing reefs, and additional reefs and platforms are found in the southern and south-eastern sections of the group. East and West Wallaby are the largest and highest islands of the Abrolhos Group.

South of the Wallaby Group, and separated from it by the Middle Channel, 25 to 26 fathoms deep, is the *Easter Group*, whose main feature is the presence of a discontinuous outer rim of reefs and platforms, sometimes crowned with islands. Inside this ring are irregular platforms and reefs and an almost centrally situated major island, Rat Island, which, however, is smaller and lower than the larger islands to the north.

Finally, the southernmost group of islands is the *Pelsart Group*, which is rather similar to the Easter Group, but with the inner reefs and platforms more irregularly scattered and with no well-defined central island, unless the very small Middle Island be regarded as such. The outstanding geographical features of the Pelsart Group are Pelsart Island, a long rim island forming the eastern margin of the group and the great reef barrier on the western side which is continuous with Pelsart Island in the south.

This reef, together with Pelsart Island, forms a continuous rampart around two-thirds of the circumference of the group, so that the lagoon inside it is only accessible through a few passages in the string of islets and reefs which mark the northern boundary of the group.

Some outlying islets and reefs will be described at a later stage when the relief of the shelf in the vicinity of the Abrolhos Islands will be discussed.

The chief emphasis, in the following, will be placed on the description of certain parts of the Wallaby and Pelsart Groups, which are the only ones in which I have carried out any investigations.

#### PREVIOUS INVESTIGATIONS.

After the discovery of the islands in 1617, a long period of time elapsed before they were surveyed and the waters around them charted. Ships were wrecked on the islands, but it was never of their own free will that men landed on their shores and these disasters contributed little to the knowledge of the islands. Two crude maps of the Pelsart Group drawn by members of the crew of the *Zeewyck*, which was wrecked there in 1727, were not published until 1899 (Heeres).

\* Joubin's map of the distribution of coral reefs (Joubin, 1912, Map 3) shows coral reefs near the mainland of Western Australia south of Geraldton, approximately between  $29^{\circ}$  and  $30^{\circ}$  S. Lat. Although, as mentioned later, some species of reef corals grow along this coast, true living coral reefs seem to be absent.

In 1840, the British Admiralty despatched the *Beagle*, under the command of Captains Wickham and Stokes, to the coasts of Western Australia, and it was on this occasion that Houtman's Abrolhos were first mapped and that their nature as coral islands was determined. The *Beagle* spent some time in all parts of the archipelago and both Wickham and Stokes published accounts of this expedition.

Wickham, in 1841, stated that the islands consist of "calcareous limestone of which the principal ingredients appear to be coral and shells". He gave a brief description of the various groups of islands which contains little of geological interest, though he commented on the difference between those islands that are built of loose corals and shells and which are mainly found on the eastern side of the island groups, and the outer islands which consist of "flat blocks of limestone about five feet above water".

It is interesting to note that Charles Darwin, who himself never visited the Abrolhos Islands, relied on information and geological specimens supplied by Wickham when, in his book on coral reefs published in 1842, he hesitated to regard the islands as atolls, leaving their proper classification in doubt.

The report by Stokes was published in 1846 and is a detailed narrative of the expedition giving a general description of all the major islands visited by the author, but there are only occasional references to matters concerning the physiography and geology of the islands. In his description of Pelsart Island is probably to be found the first reference to the occurrence of guano on the Abrolhos. Frequent reference is also made to the abundance of coral growth in the shallow parts of the sea surrounding the major islands and in the lagoons inside the outer barriers.

During the following forty or fifty years much guano was taken from the islands, but practically no further contributions towards their natural history were made. In 1897, Wells estimated the guano resources of the Abrolhos Islands at about 100,000 tons. Maitland and Jackson, in 1904, gave a review of the development of the guano industry up to that time, from which it appears that between 1876 and 1903, 92,342 tons of guano had been obtained from the islands, though much guano must have been removed prior to 1876.

The first naturalist to visit Houtman's Abrolhos was W. Saville-Kent, who spent some days in the Pelsart Group, apparently mainly on the southern part of Pelsart Island, of which he gave a somewhat detailed description in his book *The Naturalist in Australia*, published in 1897. He describes the rocks of the island as "hard coral limestone conglomerate" and deals at some length with the formations of living corals found near Pelsart Island and on the Pelsart Reef.

His account is illustrated by some excellent photographs, among which the pictures of beach formations of shells and corals may be particularly mentioned. His description and illustrations of the "birth of a coral island" by the accumulation of dead corals on a submerged reef near Gun Island are likewise of lasting interest. Saville-Kent states that plutonic rocks, similar to those found on the mainland, are known from the Wallaby Islands—a statement which proved to be in error, although it was repeated by Helms. It appears that Saville-Kent himself did not visit the Wallaby Group and he does not give the source of information for his statement.

The next visitor with geological interests was R. Helms, who published an account of the islands in 1902. Helms described briefly the guano deposits of Rat, Pelsart and Gun Islands and the methods of their recovery and shipment. Some pages of his report deal with the physiography of the islands, though the author's notions in this regard are not always free from errors. The rock formation of the islands is compared to the coastal limestone between Perth and Fremantle which the author believes to be a coral rock. Helms also states erroneously that the "Pelsart Group marks the southernmost limit at which reef-building coralpolyps at present exist"—a slight inaccuracy which has often been repeated. Helms observed that the Pelsart and Easter Groups have the appearance of atolls, but are really fringing reefs. From the presence of wallabies and other land animals (snakes) on the Wallaby Islands, Helms concluded that the Abrolhos Islands must previously have been connected with the mainland.

A more comprehensive survey of Houtman's Abrolhos was undertaken by W. J. Dakin on two trips, in 1913 and in 1915, on which Dakin reported in a preliminary way

in 1915 and more fully in a paper published in 1919. Already in his first report Dakin corrected the mistaken notion of the occurrence of crystalline rocks on the Wallaby Islands and stated that these islands, like all others of the Abrolhos group, are entirely composed of coral formations. He concluded that a comparatively recent uplift to the extent of 8 feet had taken place in the islands and that they were at present being subjected to erosion.

In his paper in 1919, Dakin gave a fuller account of the islands with notes on the hydrography of the ocean surrounding them. Outlines of the physiography of all the major islands and of many of the smaller islets and reefs, and preliminary observations on the marine fauna as well as the land fauna, are given. Up to the present time Dakin's paper is the only available coherent account, however brief, of the geology and physiography of the Abrolhos Islands and frequent reference to this author's observations and conclusions will be made in the following pages. It may, therefore, suffice here to state that Dakin regarded the Pelsart Group as an atoll and considered that the Wallaby and Easter Groups represented stages in the formation of such an atoll. He also thought that it is possible that North Island will eventually develop along the lines indicated by the three other groups. As to the age and origin of Houtman's Abrolhos, Woodward, in 1891, thought that they were composed of Tertiary limestones and Dakin suggested (1919) that they were built on a foundation of Tertiary limestone. Both Helms and Dakin claimed that the islands must once have been connected with the mainland in which assumption they received the zoogeographer's support (Alexander, 1922). Dakin explained the present features of the Abrolhos Islands as being due mainly to intense river erosion by which the island groups had been separated not only from the mainland, but also from one another. Neither of these authors gave an indication of the possible age of the islands.

#### SCOPE OF PRESENT INVESTIGATIONS.

In the beginning of 1944 I paid two visits to the Abrolhos Islands. In January, I spent almost three weeks on Pelsart Island, as a guest of the British Phosphate Commissioners. I am much indebted to Mr. R. L. Nevile, the local manager of the B.P.C., who did everything in his power to make my stay on the island pleasant and profitable. In February, I was able to visit the Wallaby Group where I spent four days each on East Wallaby and West Wallaby Islands.

My work was almost entirely confined to these three islands and such parts of submerged reefs and platforms as could be reached by wading out from the dry land. While the circumstance that no vessel was available with which submerged coral formations and more distant reefs, platforms, rim islets, or smaller limestone islands could have been studied was in some ways felt as a handicap, it is hoped that the study of many other geological features might have benefited from the enforced limitation to a few of the largest and probably most typical of the islands of the entire group.

Heights were determined by Abney level or measuring rod, distances by pacing. The map of Pelsart Island was first constructed from pace and compass traverses, with later corrections from aerial photographs placed at my disposal by the Department of the Army.

These investigations were carried out while I was on the staff of the University of Western Australia. Travelling expenses were defrayed by the Commonwealth Research Grant.

#### TIDES.

In coral islands knowledge of tidal conditions is essential for various reasons:

(1). The range of the tides determines the range and distribution of intertidal animal and plant communities.

(2). The nature of sedimentation processes in the tidal zone (accumulation of shingle, sand, calcareous mud, etc.) depends to a certain extent on the range of tide, because the latter determines the extent to which coastal platforms and reef crests are submerged during high tide.

(3). Low-water level usually determines the upper limit of vigorous coral growth.

(4). At low tide large parts of the shore platforms and of reefs are exposed so that their geology can be studied.

(5). It is necessary to have a datum line to which elevations can be related. Considering the low heights of the islands irregularities in the tides constitute sources of error of which the observer must be aware.

The Admiralty Chart gives a spring rise of  $2\frac{1}{2}$  feet in Middle Channel, between the Wallaby and Easter Groups. During my stay on Pelsart Island I found the spring range to be nearer 3 than  $2\frac{1}{2}$  feet, which means that spring rise above datum would certainly be more than 3 feet. From observations made by Mr. R. L. Nevile there can be little doubt that exceptionally the spring rise is even higher.

On the mainland coast near Geraldton the Admiralty Chart notes a spring rise of  $1\frac{3}{4}$  feet. However, north of the mouth of the Bowes River, 23 miles north of Geraldton and due east of the Wallaby Group, I found indications of a range of tide decidedly in excess of 3 feet, and probably nearer 5 feet.

Such disconnected observation may serve to show that tidal conditions seem to vary even over comparatively short distances, but more continuous and accurate observations are badly needed.

An interesting problem is presented by the time of arrival of the tides. During my stay on Pelsart Island between 19th January and 8th February, 1944, low tide always occurred in the early morning and the tide did not start to come in until 8 or 9 a.m. High water was reached during the afternoon with the highest level around 6 p.m. On one day, however (7.ii.44), the tide did not rise appreciably during the morning, low tide conditions prevailing until well after 12 noon. It is interesting to note in this connection that Dakin (1919) remarks on the peculiar fact that on both his trips to the Abrolhos Islands (October, 1913, and November, 1915) low tide occurred between 6 and 8 a.m., very much as in January, 1944.

Halligan (1923, p. 717) stated that along the whole of the coast of Western Australia from North-West Cape to Cape Leeuwin it is high water between the hours of 2 and 4 o'clock (Greenwich time), that is, between 10 a.m. and 12 noon Western Australian time, which does not agree with Dakin's and my own observations on the Abrolhos Islands. Curlewis (1915) has analysed tidal observations at Fremantle Harbour and found the tides to be highly irregular, with no apparent connection between arrival and range of the tides and the age of the moon. Halligan pointed out that the behaviour of the tides along the Western Australian coast does not fit in with any theory of tidal phenomena so far stated.

A curious anomaly in the time of the tides which may serve to illustrate these conditions was observed in February during my visit to the Wallaby Group. Prior to 28th February, 1944, I was unable to make connected tide observations. On this day, however, I noticed that after low tide at the usual hour early in the morning, the water rose rapidly after about 8 a.m. and reached its highest level between 12 noon and 1 p.m. After 1 p.m. the water level fell slowly and at 6 p.m. it was almost down to low water level. There was no second high water during the night. After dark the water must have continued to fall slowly and low water must have occurred sometime between 6 p.m. and 6 a.m. These conditions were repeated during the following days until 2nd March, 1944, but on 3rd March, 1944, the tide suddenly returned to "normal" and high water did not occur until late in the afternoon.

During the months of January and February the Abrolhos Islands are situated in the trade-wind belt and the wind blows steadily and strongly from south to south-south-east. Irregularities in the behaviour of the tides were, therefore, not caused by changes in the direction of the wind.

It is perhaps also worth recording that when the *Windsor* suffered shipwreck on the outer reef of the Pelsart Group in February, 1908, the rescue party was able to remain on the reef all day, and during one night, people from the *Windsor* stayed on the reef, sheltering in the lee of "coral outcrops" (Uren, 1940, p. 107)—something which would have been altogether out of the question at any time during my stay on Pelsart Island.

It is obvious that such irregularities in the tidal conditions must influence adversely the accuracy of levels taken, for moving about on the islands one is often in doubt about



the datum level to which to refer. It has been stated, for example, that the outer reef of the Pelsart Group is "almost always" submerged, an impression which can easily be obtained on some days, whereas there can be no doubt that the surface of the reef stands at least two feet above datum.

Irregularities in the arrival and ranges of the tides may also seriously upset plans for the investigation of reefs and submerged platforms.

#### GEOLOGICAL FORMATIONS.

In the following the different types of rocks and loose deposits of which the islands are composed will be briefly described. Some of these formations are the results of geological processes which are now concluded, others are still in the process of formation. Throughout this investigation, however, I have concentrated on the geological rather than the sedimentological aspect, although I am well aware that the two cannot be well separated. However, the arrangement, composition, distribution and mode of origin of the rocks and loose deposits that make up the islands to-day have received first consideration; processes of present sedimentation around and near the islands have only been studied incidentally, since more time and equipment would have been necessary for this purpose.

Perhaps reference should be made first of all to a rock type which is *not* represented on the Arolhos Islands, viz., beach rock, or beach sandstone, which has been described from many coral islands all over the world. Although sandy beaches are not very prominent in the Arolhos Islands, they are not at all absent. A continuous sandy beach lines the southern and most of the western side of East Wallaby Island and such beaches are also found on West Wallaby Island, particularly along the northern half of the west coast, but no beach rock was ever seen.

#### REEF LIMESTONE.

Coral reef limestone forms the foundation of every island in the Arolhos Group (Pl. ix, fig. 1; Pl. xiv, fig. 4). In many places this coral limestone base does not reach high-water level and is overlain by younger formations such as coral shingle, coquina beds, or shell limestone of which some of the islands entirely consist. Elsewhere the coral limestone is raised several feet above high-water level and some islands consist entirely or partly of such raised coral rock which may or may not be overlain by younger deposits.

Although coral limestone is the most widespread of the geological formations of the Arolhos Islands, there is little need to describe it here in great detail, since it does not present any unusual features. It consists predominantly of the skeletons of the same species of corals which are still found in the same neighbourhood, the colonies occupying the position in which they grew. The spaces between the coral colonies are filled with coral débris, shells and shell grit, cemented together into one solid mass by deposits of secondary calcite and partly perhaps already by algal action when the reef was still alive.

In some places in the vicinity of the Wallaby Islands the coral limestone contains pockets of grey-coloured fine-grained limestone with shell remains.

The surface of the reef limestone is somewhat uneven, as might be expected, and existing depressions or pockets are mostly filled in with coral débris. It is very often impossible to separate clearly such "coral débris limestone" and the original reef limestone as one merges into the other, and limestone made up of coral fragments derived from *in situ* clastation of reef corals, which have obviously never been transported to any marked degree, is here included in the reef limestone.

#### SHELL LIMESTONE.

In many places the basal reef limestone is covered by a layer of limestone, seldom more than 3 feet thick, in which coral fragments are conspicuously rare and which is mainly characterized by shell remains (Pl. ix, fig. 1). This limestone is fine-grained, sometimes massive, sometimes bedded; it rests on an irregular surface of reef limestone and is truncated above by a flat surface which forms the top of all elevated limestone

cliffs and the basis on which all later deposits such as dune limestone, beach ridges, shingle limestone, etc., have been deposited. In places the limestone may grade into consolidated shell grit, but mostly it consists of a rather dense groundmass in which shells and fragments of shells are embedded. These shells are sometimes the same as those which are now found along the coast of the same islands, but sometimes the limestone fauna differs markedly from recent assemblages, as e.g., in the southern half of Pelsart Island.

The most remarkable aspect of this limestone is the general scarcity of coral remains in it; although they may occur locally, they never contribute materially to the mass of the rock. It seems, therefore, that this limestone was formed at a time when not much coral growth was going on in the islands. There was consequently little supply of broken-off coral fragments and the main source of the limestone deposit was pre-existing coral rock and contemporaneous shells.

#### SHINGLE LIMESTONE.

Shingle limestone may be considered separately from loose aggregates of coral shingle, such as beach ridges and others. As shingle limestone I propose to classify rocks that result from the cementation of intertidal deposits largely composed of coral fragments. As far as the Abrolhos are concerned a clear distinction between shingle beach ridges and shingle limestone has always been easy to make, for nowhere were consolidated beach ridges found, and shingle limestone deposits were usually of such a nature as to suggest formation in the zone of breakers, slightly outside the zone in which beach ridges are built.

Typical deposits of shingle limestone are found in many places on Pelsart Island where it may be up to 4 feet thick (Pl. xi). This limestone is almost exclusively composed of fragments of *Acropora* species and as a rule there is a distinct sorting of the material. The rock is distinctly bedded (Pl. xii, fig. 4) and there is often a definite change in the size of the coral fragments from one bed to another. Some beds are composed of more or less strongly rolled and worn pieces of branching species of *Acropora*, whereas in others slabs of fan- or disc-shaped species predominate. The latter were sometimes found to be arranged in the characteristic roof-tile fashion which is also observed in recent coral accumulations, and which furnishes proof of the formation of the deposit under water in the surf zone.

Shingle limestone is usually found resting on a reef limestone platform. It is mostly overlain by unconsolidated shingle beach ridge formations. The break between the shingle limestone and the beach ridges is always evident and I have never seen any gradual passage between the two. It must therefore be supposed that sufficient time elapsed between the deposition of the two to allow the shingle limestone to harden to some degree. As already mentioned, no cementation has affected the beach ridge material and the consolidation of the shingle limestone must, therefore, have been completed before the beach ridges were deposited on top of it.

Stephenson *et al.* (1931) have described a similar rock type as "shingle conglomerate". This, however, refers to recently cemented platforms of coral debris and the term "shingle limestone" is here preferred in order to emphasize the greater age of these deposits.

#### DUNE LIMESTONE.

Dune limestones were found on East Wallaby and West Wallaby Islands (Pl. xv), and from the account of North Island given by Dakin in 1919, it can be concluded that similar limestones are also present on that island.

The dune limestone commonly rests on shell limestone platforms, raised several feet above sea-level, so that its base is now everywhere from 5 to 8 feet above H.W.L. The greatest thickness observed was on West Wallaby Island, where on the south coast the dune limestone is up to 30 feet thick. The limestone consists of very fine-grained calcareous material, viz., the finely-ground remains of corals, shells, echinoids and Foraminifera. Its texture is fairly homogeneous and cross-bedding is rarely recognizable.

One of the most noticeable features of the dune limestone is the occurrence, in distinct horizons, of a mesh-work of branching bodies which weather out readily on exposed faces of the limestone (Pl. xv, fig. 3). The branching bodies consist of denser limestone than the surrounding rock and sometimes the calcium carbonate is arranged in concentric layers when seen in cross-section. Considering the general arrangement of these branching structures, there can be little doubt that they are the remnants of root systems which once penetrated the dune sand before it was hardened into limestone. The process probably took place in such a way that at first the roots were surrounded by an encrustation of calcium carbonate or by a hard crust of grains cemented together by secondary calcium carbonate, possibly formed as the result of some moisture or solutions penetrating into the sand from the roots. That processes of this kind are still going on can be observed in many places on the coast of Western Australia, notably on Penguin Island, where dead roots are being encrusted in this way in a small dune which forms on the southern half of this little island. The next step would be the disappearance of the organic matter and the filling of the resulting cavity either with more dune sand filtering in from above, or with secondary calcareous deposits which may be deposited in concentric layers.

Occasionally it can be seen that a system of root structures is abruptly cut off at a certain level, indicating a surface of the dune which has been stable for some time. Thus, on the south coast of West Wallaby Island three such horizons can be observed (Fig. 5).

The surface of the dune limestone deposits on the Wallaby Islands is always more or less strongly undulating, as can be seen particularly well along the south coast of West Wallaby Island and along the east coast of East Wallaby Island. The root horizons have the same inclination as the surface of the limestone deposits and in some places the surface layers of the limestone consist of a root horizon. It is, therefore, obvious that the undulating surface of the limestone deposits is original and not due to erosion.

These dune limestones must have been formed under physiographic conditions which were somewhat different from those of the present day. The dune limestones are now everywhere subjected to erosion, forming steep coastal cliffs, so that it is obvious that when they were formed the islands on which they occur must have been larger than now. These limestones are sometimes overlain by recently cemented dune sands of the present physiographic cycle from which, however, they can always be readily distinguished. These cemented dune sands will be described below.

The remarkable resemblance of the dune limestones of the Arolhos Islands to certain parts of the Coastal Limestone of the mainland of Western Australia became increasingly obvious during the present investigations. The Coastal Limestone will therefore be briefly discussed in a later section of this paper when reasons for the correlation of its subaerially-formed part with the dune limestone of the Arolhos will be given.

It may be worth recording that the occurrence on the Arolhos Islands of dune limestones similar to those of the mainland was already suspected by Charles Darwin in 1842, in his *Origin and Distribution of Coral Reefs*. Darwin saw some limestone specimens collected by Captain Wickham during his survey of the islands in 1840. "These", he writes, "closely resembled a formation at King George's Sound, principally due to the action of the wind on calcareous dust, which I shall describe in a forthcoming part." This description appeared in 1844 in Darwin's *Geological Observations on Volcanic Islands* and will be referred to in another section of this paper.

#### LITTORAL DEPOSITS.

##### *General Remarks.*

Along a coast where corals grow in the vicinity of the surf zone, there is a continuous supply of broken-off coral fragments and colonies which are thrown on to the tidal platform by the waves or carried along the shore by shore currents. Some of this material is deposited under water, or at least in places like the tidal platform which are covered by water during high tide. This material is in an unstable position;

the deposit may be broken up at any time by larger waves and the fragments may then be redistributed along the coast or thrown on to the beach beyond the range of ordinary waves. The deposits thus formed are much more stable under ordinary conditions and a wall is formed along the innermost edge of the surf which is known as beach ridge. Beach ridges are heaped up along the inner edge of the surf, mainly by the action of strong waves during storm periods, and thus just somewhat out of reach of the ordinary waves. The peculiarity of beach ridges is that they are borderline cases between marine and subaerial deposits: they owe their origin to the action of the water, but once built they are immediately exposed to the atmospheric agents and, unless degradation of the coast takes place, they are not acted upon further by the waves. It is, therefore, advisable to consider the littoral deposits of coral islands under two headings:

(1). Subaqueous shingle deposits which are either covered by every high tide or are at least within the reach of the "normal" surf.

(2). Beach ridges.

(1). *Intertidal Shingle Deposits.*

As has already been explained, such deposits are unstable. They consist of coral material which is constantly being thrown up from the edge of the growing reef. Branching colonies are broken up into cylindrical fragments which are rolled about and smoothed down and are often found with their long axes oriented in the direction of the wave. Dish- and fan-shaped colonies are usually broken off whole. As soon as they are thrown on to the tidal platform they are turned upside down, because their upper surface is usually flatter than the lower surface which forms a short massive stalk by which the colony was attached to the substratum. In this inverted position the coral specimens which may be very heavy, measuring up to four and five feet in diameter, are pushed shoreward towards the edge of the surf zone where they are piled up in a characteristic roof-tile arrangement (Pl. x, fig. 4). These very large specimens are not normal constituents of beach ridges, because apparently extraordinarily strong waves are required to throw them up on the beach. Interbedded with this "roof-tile" shingle are the cylindrical fragments of branching corals. Shells are conspicuously absent from such deposits, because shells which remain in this zone of deposition for any length of time will soon be broken and ground down between the heavy and massive coral slabs. Shells may, however, be transported rapidly across this belt and may be incorporated in the marginal beach ridge where they are occasionally surprisingly well preserved.

This material on the tidal platform is constantly exposed to the action of the waves. It is rolled about and worn down and to some extent it may be shifted along the coast by shore currents set up by the oblique onrush of the waves. It will be shown later how important the coastal drift of coral shingle is for the growth of rim islands in a longitudinal direction. Eventually some of this material will be incorporated into the beach ridge which lines the shore.

A word must be said here about the coral shingle accumulations that have been described as "ramparts" from reef platforms in the Great Barrier Reef and in the Dutch East Indies (Steers, 1929; Spender, 1930; Stephenson *et al.*, 1931; Umbgrove, 1928-39; Kuenen, 1933). Ramparts are ridges of coral debris built up by wave action on platforms and more or less completely submerged at high tide. Unlike beach ridges which they resemble, ramparts are regularly covered by the tide, although some exceptionally high parts may be dry at all but the highest tides, or even, particularly in old rampart systems, be permanently dry. Ramparts are subjected to wave action and during storm periods they are moved bodily inward. This movement continues until a new rampart is built on the outside which takes the brunt of the onrushing waves and protects the older rampart which then becomes stabilized. Such systems can only develop on a stable foundation and under conditions of stationary sea-level. Intertidal deposits of the rampart type are unknown from the Abrolhos Islands, at least from the major islands which I have studied. They may, of course, be present elsewhere. It is, however, possible that it is due to the small tidal range that coral shingle ridges tend to be built

up to an appreciable height above high-water level and thus acquire the characteristics of beach ridges.

## (2). *Beach Ridges.*

The accumulation of beach ridges of coral shingle is probably due mainly to the action of storm waves during high tides when coral material and shells are thrown up onto the beach where they are put out of reach of the action of ordinary waves. The formation of a coral shingle beach ridge depends on a number of factors of which the most important are: (a) the amount of coral material supplied by the off-shore coral reef, (b) the width of the tidal platform, which determines to a large extent the size and intensity of the waves reaching the shore at high tide, (c) the range of the tide, which determines the degree of submergence of the tidal platform during high tide, (d) the intensity of the long-shore current during high tide, (e) the behaviour of the foundation on which the beach ridge is being built, whether rising or stationary or subsiding. Only the last three factors are of regional importance. The other two may vary from place to place along a coastline and the result will be that, on a stationary foundation, new beach ridges may be accumulated in one place whereas simultaneously existing beach ridges may be degraded at another place. Such conditions are prevalent along the each cost of Pelsart Island and will be discussed in greater detail in the later description of that island.

Coral shingle beach ridges consist of unsorted material. The coral fragments are arranged in all directions so that they form a densely packed and firmly interlocked mass which is not likely to undergo any further compaction when, in the later stage of its development, it is removed from the influence of the waves. Mixed with the coral fragments is a certain amount of more or less abraded gastropod and pelecypod shells, generally heavy shells of the rough water type such as *Turbo*, *Trochus*, *Chama*, *Tridacna*, etc. To these are added occasional echinoid tests, sponges, bryozoan skeletons, foraminiferal tests, etc., but such material is very subordinate (Pl. xii, figs. 1, 2).

The beach ridges are built up to a height of 5 or 6 feet; at least no higher ridges have been observed along the coast of Pelsart Island, where they are best developed. At some distance from the shore the older beach ridges usually attain a greater height, but this is believed to indicate an emergence of the island.

One of the most outstanding features of coral shingle beach ridges is the progressive blackening of the surface of the coral fragments. That coral shingle exposed to the air gradually acquires a black surface has been noted by several observers, e.g., by Hedley (1925), but to my knowledge this feature has never been described in detail nor has an attempt been made to explain it.

When freshly washed up on the beach, coral fragments are white, sometimes with a slight yellowish tinge, and if beach ridges are of this colour, it can be assumed that they are still in the process of formation. Beach ridges which have been exposed to the air for some time take on a slightly greyish coloration which becomes increasingly darker in time. This progressive blackening of the coral shingle can be well observed in some places on Pelsart Island where four or five different systems of beach ridges have been formed parallel to the coast.

On slightly older beach ridges the grey colour of the surface becomes darker and at the same time weathering of the surface of the coral fragments, brought about by the action of dew, rain and ocean spray, becomes evident. As one proceeds to older beach ridges both the blackening and the weathering are intensified so that on the oldest beach ridges observed on Pelsart Island the colour is very dark grey and at the same time the coral fragments which cover the surface have been converted into blackened, pitted, and jagged pieces whose coral nature is often hardly recognizable. Also, on these older ridges there is an increasing growth of lichens on the surface and at the same time the scrub vegetation advances from inland and begins to creep over them. The material of the older ridges has become very brittle and pieces snap off easily when trodden upon; this is probably due to the fact that part of the calcium carbonate of the coral skeleton has been carried away in solution. The whole mass of the coral shingle, at least in the surface layers of the ridge, has thus become more porous.

Shells are somewhat differently affected by these processes of blackening and weathering. They never become quite as dark as the coral fragments and it is mainly the outer, prismatic layer which is affected. On the older ridges the prismatic layer of mollusc shells becomes very brittle and gradually disintegrates, but the nacreous layer which only acquires a slight greyish tinge is much more resistant and is well preserved even on the oldest ridges.

It remains to consider the question of the origin of the blackening of the corals. In this connection three observations are important: (1) The blackening only affects a narrow surface zone of the coral fragments whose interior remains white; (2) it only affects the coral fragments in the uppermost four or five inches below the surface of the coral shingle accumulations; deeper down the fragments have a yellowish tinge with no trace of grey; (3) the blackening is much less intense or even absent where the surface of the beach ridge is covered by objects thrown on top of it such as drift timber, whale bones, etc.; all these observations suggest that organic agents might be responsible for the blackening of the shingle.

When some of the blackened coral was dissolved in hydrochloric acid, an abundance of dark green particles remained which Miss A. Baird, of the Botany Department, University of Western Australia, determined as cells of blue-green algae (Chlorophyceae) mostly of the *Chroococcus* group. Miss Baird suggested that gradual weathering of coral shingle prepared the ground for the colonization of its surface by the algae. This explanation seems very reasonable and is here accepted. It is, therefore, suggested that the blackening of the coral shingle is due to the colonization of the surface of the coral fragments by blue-green algae; this proceeds as quickly as the weathering of the surface of the specimens will permit. Under flotsam thrown onto the surface of the shingle, weathering, which, as has been explained, is entirely due to rain, atmospheric moisture and spray, will be slower and the algal growth will be retarded so that in such places the shingle surface remains a lighter colour.\*

Since the conditions which lead to the blackening and weathering of the coral shingle are uniform over the entire area of the Abrolhos Islands these processes must go on at very much the same rate everywhere, and it is, therefore, possible to correlate beach ridges in different parts of an island, and probably also on different islands, with the help of these features.

An approximate idea of the age, and therefore of the time required for the formation of the beach ridges, can be obtained from an observation of certain associated features such as drift wood and the like. Modern beach ridges and beach ridges which show only initial blackening are abundantly covered by flotsam in the form of ships' planks, boxes, boards and the like. These objects decrease rapidly in quantity as the older beach ridges are approached. This suggests that the youngest beach ridges must have been formed since the time when more or less regular shipping began along this part of the coast of Western Australia, that is, approximately during the last hundred years or so. The time that is required for the first signs of blackening of the shingle to appear can be deduced from certain observations in old guano workings on Pelsart Island. Here much of the old shingle surface has been disturbed and unblackened shingle from below has been mingled with blackened surface specimens. Nowhere have I been able to observe any sign of initial blackening of the recently uncovered coral fragments, except in the south-west corner of the old guano field on the southernmost part of Pelsart Island. It is known that guano was taken from the Abrolhos Islands prior to 1847, probably soon after its discovery by Wickham and Stokes' expedition, although no records exist of these early activities. It is obvious that the

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\* Some considerable time after the completion of this manuscript, I discovered that the presence of Chroococcaceae in weathered limestone has previously been noted by Diels, as quoted in a paper by K. Andrée, "Verschiedene Beiträge zur Geologie von Canada" (*Schr. Ges. ges. Naturw. Marburg*, Vol. 13, 1914, p. 422). Andrée describes in some detail the role played by algae in the superficial weathering of limestone and concludes that algae actively destroy the rock, both chemically and mechanically. It will be seen that these findings are at variance with the suggestions offered above. Possibly, as Andrée himself admits, both organic and inorganic agents are at play.

dumps which show the beginning of blackening of the coral fragments of the surface must have been made at a very early period. They may be about 100 years old.

On the east coast of Pelsart Island, near Mangrove Bay, a ship, the *Ben Ledi*, was wrecked in 1879. Much wreckage was thrown onto the beach where it is still spread out along the shore covering the outermost beach ridge which is now being eroded by the waves. The shingle of this ridge shows initial signs of blackening, but there is no marked difference in the blackening of those parts that have been covered by flotsam, indicating that a period of 65 years has been insufficient to produce a very noticeable increase in the intensity of the blackening of the shingle.

Both lines of evidence, that is, the time required for the first signs of blackening to appear and the amount of flotsam thrown onto the ridges, point to an age of the youngest beach ridges of not less than about 100 years, probably more. Nowhere is there any evidence that more than two beach ridges have been formed during this period and in most places there is only evidence of one.

The amount of flotsam decreases rapidly on the older beach ridges and the oldest ridges are entirely free from any flotsam of man-made origin. It is reasonable to conclude that they, therefore, were formed prior to the arrival of European ships in the Indian Ocean, that is, they must be older than about 400 or 500 years.

#### COQUINA AND SHELL SAND DEPOSITS.

These are typical deposits of the inside of larger islands, that is, of that side which is facing away from the open ocean. Thus, on Pelsart Island, coquina and shell sand deposits are prominent along the west coast, on West Wallaby Island on the east and south coasts. However, where outer coasts are protected by outlying reefs or wide coastal platforms such sediments may also accumulate there as, e.g., along the northern part of the west coast of West Wallaby and along the southern part of the west coast of East Wallaby. Their accumulation to a large extent depends on the existence of tidal currents parallel to the shore and very often takes place in the form of sand spits and sand bars which are in many places still in the process of formation.

There are all stages of transition between pure shell beds and sands composed of finely-ground fragments of shells. In places such sands may have an admixture of guano and may then even grade into pure guano deposits. Bedding is usually not too evident, although alternations of shell beds with layers of shell grit have been observed.

Deposits of this type will be described in more detail later on.

#### GUANO AND ROCK PHOSPHATE.

No special study of these deposits was made, since the greater part of them has long been removed from most of the islands. Wherever guano deposits have been worked, the ground is now much disturbed and it is usually impossible to obtain a picture of the original relations of the various surface deposits. The main deposits occurred on Pelsart Island, Rat Island and West Wallaby Island, but many of the smaller islands have also yielded guano in the past. The guano seems in most places to have accumulated in depressions, either in old lagoons, or in valleys between dune limestone ridges, or on raised limestone platforms inside the ring formed by the marginal beach ridge surrounding such platforms. Much of the guano has been of good quality, but there are all gradations from the pure product to guano-bearing sands and shingle deposits of no commercial value.

In some places phosphate that has been leached out of the guano has penetrated into underlying deposits to form rock phosphate. Thus accumulations of shells and coral shingle may be cemented together and the shells and coral skeletons be phosphatized to a greater or lesser degree, but such deposits have apparently rarely been of any great extent.

#### DUNES.

Dunes are not important in the geological picture of the Abrolhos Islands. They are found to any extent only on East and West Wallaby Islands and, according to Dakin, on North Island. Their formation is obviously closely connected with the existence of sandy beaches. Where beach sand accumulates, dunes are likely to be

formed along the shore. Dunes are usually absent along shingle and cliff coasts, because not enough fine-grained material is available from such sources.

More than on any other island, sand beaches are developed on East Wallaby Island, and it is here that we also encounter the most extensive dune formation; minor dunes are found capping the dune limestone along the south coast of West Wallaby Island. On Pelsart Island a thin cover of wind-blown sand, barely sufficient to cover the shingle surface, is found here and there, but only in one place has such sand accumulated to form low dunes, three or four feet high.

Dune sands on the Abrolhos Islands consist entirely of calcium carbonate material and are, therefore, liable to cementation by percolating water. Such cementation was observed in the vicinity of Flag Hill, East Wallaby Island, and elsewhere, but the resulting rock is usually friable and can be crushed between the fingers. It is easily distinguishable from the older dune limestone which it usually overlies and which is much harder.

#### RECENT CORAL FORMATIONS AND CONDITIONS FOR CORAL GROWTH.

Dakin and others have described the luxuriant growth of reef corals in many parts of the Abrolhos Islands, but, as has already been explained, my own facilities for observations of this nature were limited to the immediate vicinity of the islands visited by me.

Although various expeditions have collected corals on the islands, some on a much more extensive scale than I was able to do, no list of coral species of the Abrolhos Islands has ever been published. The following list of corals collected around Pelsart Island and on the Pelsart Reef may supply some of the wanted information:

<i>Pocillopora</i> cf. <i>bulbosa</i> (Ehrenb.).	<i>Favia speciosa</i> (Dana).
<i>Acropora decipiens</i> (Brook).	<i>Favites virens</i> (Dana).
<i>Acropora</i> cf. <i>scherzeriana</i> (Brugg.).	<i>Favites favosa</i> (Ellis & Sol.).
<i>Acropora</i> cf. <i>gemmifera</i> (Brook).	<i>Hydnophora exesa</i> (Pall.).
<i>Acropora</i> cf. <i>pallifera</i> (Lam.).	<i>Platygyra lamellina</i> (Ehrenb.).
<i>Acropora</i> cf. <i>pectinata</i> (Brook).	<i>Platygyra daedata</i> (Ellis & Sol.).
<i>Acropora</i> cf. <i>haimi</i> (Brook).	<i>Cyphastraea serailea</i> (Forsk.).
<i>Acropora</i> cf. <i>grandis</i> (Brook).	<i>Leptastraea</i> cf. <i>transversa</i> (Klz.).
<i>Montipora</i> cf. <i>venosa</i> (Ehrenb.).	<i>Galaxea musicalis</i> L.
<i>Porites solida</i> Forsk.	<i>Euphyllia</i> , n. sp.

This list is neither very complete nor very accurate. Probably it will eventually be increased by at least another five or six species. In the beginning of 1945, I was fortunate enough to be able to study coral collections from the Great Barrier Reef of Queensland in the University of Queensland and in the Queensland Museum, and it seemed to me that there are several coral species among the Abrolhos faunas which may not be known from the Great Barrier Reef and which are possibly new to the generally well-known Indo-Pacific coral fauna.

The number of species that constitute the coral fauna of the Abrolhos Islands is small compared with that of tropical faunas. For example, no less than 96 species are found in the coral reefs of the Bay of Batavia, and 88 species have been reported from Amboina (Umbgrove, 1939).

This reduced number of species in reefs of the marginal zone of the coral reef belt is perhaps not surprising, because the temperature of the waters round the Abrolhos Islands must be very near the lower limit at which growth of reef corals is still possible. Schott's maps (Schott, 1935) show Houtman's Abrolhos situated on the 22.5°C. isotherm in February and on the 19° isotherm in August. According to Halligan (1930) the mean temperature for 1929 in the same general region was 69°F. and the mean temperatures for 1927 were as follows:

January to March .. .. .	71° F.
April to June .. .. .	71½° F.
July to September .. .. .	65° F.
October to December .. .. .	68° F.



In January–February, 1944, I measured the following temperatures of the water along the outer coast of southern Pelsart Island:

21.i.1944.	8.25 a.m.	.. .. .	21.8°C.
27.i.1944.	9.30 a.m.	.. .. .	21.8°C.
7.ii.1944.	8.30 a.m.	.. .. .	22.0°C.

These comparatively low mid-summer temperatures suggest that the temperature in winter might easily fall below 20°C.

On the lagoon side of Pelsart Island the temperature seems subject to great variations in the course of the day. On 22nd January, 1944, the temperature near the shore at the workers' camp was only 18.8°C. at 8 a.m., but rose to 23.8°C. at 5.45 p.m. The minimum temperature along the lagoon shore in winter must fall considerably below the observed minimum of 18.8°C. and yet at this place there is a rather vigorous growth of *Acropora*.

From the amount of shingle thrown onto the shore along the outer coast of Pelsart Island it can be concluded that there is a fairly continuous growth of corals along the slope of the coastal platform, below the low water line. The platform itself is comparatively free from coral growth, except near its edge, where occasional colonies of *Acropora*, *Pocillopora* and *Goniopora* are found.

A description of the outer reef of the Pelsart Group is given in a separate section below. Apart from this reef there is vigorous coral growth reported from many parts of the lagoon, but in this respect I must refer to the description by other authors, chiefly by Dakin (1919).

In the Wallaby Group there is little coral growth in the vicinity of East and West Wallaby Island, except along the south coast of West Wallaby Island and around Fish Point on East Wallaby Island, where a certain amount of coral shingle is supplied to the beaches.

There is, however, much coral growth in the shallow waters between East and West Wallaby Islands and on the water level reef which begins at the south-east corner of West Wallaby Island and from there runs in an arc to a point about one mile east of Pigeon Island. The end of this reef is marked by a very small shingle island which at present is growing apparently by addition of material from the south.

It seems that reef corals also grow in many places near the mainland coast and on the shelf south of the Arolhos Islands, without, however, forming coral reefs. For example, *Pocillopora* colonies grow off the breakwater of Geraldton Harbour, and I have also found the same genus in fair quantities off the coast north of the Bowes River, 25 miles north of Geraldton.

Information regarding the occurrence of reef corals on the shelf farther south is scanty. The British Admiralty charts record occasional "coral" as far south as Lat. 32° 35', and in 1907, Hartmeyer reported that colonies of *Turbinaria* had been dredged off the coast near Bunbury. I myself have collected colonies of *Pocillopora* and *Siderastraea* in tidal pools at Cape Vlaming, Rottneest Island, but the latter genus apparently does not occur on the Arolhos Islands.

On the whole, it would seem that conditions are favourable for the growth of certain types of reef corals on the Western Australian shelf at least as far south as Lat. 33° 20'.

#### GEOLOGICAL DESCRIPTIONS OF SOME MAJOR ISLANDS.

##### PELSART ISLAND.\*

###### *General.*

Pelsart Island is the longest, and at the same time the narrowest, island of the Arolhos Group (Pl. vi). From end to end it is about seven and a half miles long; it is

\* Pelsart Island was named by Wickham and Stokes on their expedition in the *Beagle* in 1840. Among the fishing population of Geraldton the island is known as "Long Island", but this is the name given by Dakin to one of the Islands of the Wallaby Group. The official usage is here adhered to.

The earliest maps of the Pelsart Group, including Pelsart Island, are those drawn by Jan Stejns and by Adrian de Graaff, two members of the crew of the *Zeeuyck* which was wrecked on the outer Pelsart Reef in 1727. These maps were first published by Heeres in 1899 and reference to them will be made later in this paper.

widest near its southern end where it is up to 600 yards wide. The narrowest stretch is found in the northern part where in one place north of Mangrove Bay the island is only 100 feet wide, but in two or three other places the island is less than 150 yards wide. The greatest height of the island is in the south where it rises to 15 feet above high-water level, but some mangrove patches in the centre of the island grow to slightly greater heights.

Pelsart Island is built on a foundation of coral reef limestone the surface of which reaches generally to about low-water level. The reef limestone platform is the continuation of the water level reef which surrounds the great Pelsart Lagoon on its eastern and southern sides. With few exceptions Pelsart Island is built of sedimentary rocks and loose aggregates derived from the coral limestone and from the skeletons and shells of corals, molluscs, etc., which live now near its shores. Significant exceptions are some small limestone platforms in the south which rise up to about 10 feet above high-water level. Here the reef limestone is overlain by shell limestone.

The geology of Pelsart Island is best considered in four different sections:

- (1). Little Island, a small islet south of the main body of Pelsart Island.
- (2). Southern Pelsart Island, from its southern tip to the beginning of the mangroves.
- (3). Central Pelsart Island, from the beginning of the mangroves to the northern end of Mangrove Bay.
- (4). Northern Pelsart Island.

The following description of the island will proceed from the south towards the north. This is the direction in which the island has grown and is still growing.

(1). *Little Island*. Pl. vii, fig. 1.

The southernmost end of what on available maps is shown as Pelsart Island is formed by a little islet which is separated from the main body of Pelsart Island by a stretch of reef flat, almost entirely dry at low water neaps and only 200 to 300 feet wide. For the sake of convenience, I propose to speak of this islet as *Little Island*. Little Island is approximately circular and about 100 yards in diameter, but, small as it is, it provides an excellent opportunity for observing a number of important features.

Little Island rises to a height of about 11 feet above low-water level (Pl. viii, fig. 2). It is surrounded by undercut limestone cliffs about 8 feet high (Pl. viii, fig. 1), except on its north-western corner where there is an accumulation of shells, mostly *Turbo* and *Trochus*, washed up on the leeward side of the island. The lower part of the limestone of the island, up to 5 or 6 feet above low-water level, is reef limestone, composed mainly of dendroid colonies of *Acropora*. This limestone is overlain by 2 to 4 feet of shell limestone which is well stratified and consists of shell grit, shells and coral fragments (Pl. ix, fig. 1). This limestone forms the flat top of the island and, near the northern edge of the island, is overlain by about 3 feet of shell and coral shingle.

The surface of the shell limestone platform has been strongly eroded, giving rise to peculiar "limestone chimneys" which rise 2 to 4 feet above the general level of the platform (Pl. ix, fig. 2) and which are carved out of the shell limestone. They have a diameter of between 30 and 100 cm., with a wall between 3 and 20 cm. thick. The inner side of the wall is coated with secondary limestone deposit which varies in thickness from a thin film to about 1 cm. In some chimneys it has partly or entirely disappeared, or perhaps it was never present. The inner side of such chimneys is strongly pitted by solution cavities. The chimneys never penetrate the limestone deeper than the top of the reef limestone though not all chimneys reach that level. They are probably old pot-holes which have been left standing owing to the reinforcement of their walls by secondary calcite deposit.

The limestone cliffs of Little Island are strongly undercut, with overhanging ledges of up to 5 or 6 feet wide. The nature of undercut limestone cliffs can, however, be better studied on the southern part of Pelsart Island.

It seems peculiar that Little Island is not indicated on Jan Stejns' and Adrian de Graaff's maps prepared in 1727 (see Heeres, 1899, pp. 93-96), although a fairly thorough

investigation of the southern end of Pelsart Island was made by them. It is possible, therefore, that in the beginning of the 18th century, Little Island was tied to the main island by shingle deposits which have later been swept away.

(2). *Southern Pelsart Island*. Pl. vii, fig. 1.

This part of Pelsart Island is made up of a variety of formations such as raised reef limestone, shingle limestone, coquina and shell sand deposits, guano, rock phosphate, shingle beach ridges, and so on. The variety of deposits is greater in this part of the island than anywhere farther north.

The southernmost portion of the island consists of an elevated limestone platform which is 1,400 feet long and 600 feet wide. This platform is crowned by a ring-shaped, continuous beach ridge, deposited close to its outer edge. Inside this ring-shaped beach ridge there were once guano deposits and some rock phosphate, all of which have, however, now been removed.

The edge of the limestone platform stands at  $5\frac{1}{2}$  to  $6\frac{1}{2}$  feet above high-water level and consists of solid reef limestone in places capped by coral débris limestone as described in a previous section. The profiles of the east (or outer) and west (or inner) shores of this platform are somewhat different. The east side rises as a steep cliff from the tidal platform which is here less than 100 yards wide. The tidal platform is highest near its outer edge where it forms the well-known *Lithothamnium* rim, rising perhaps to  $1\frac{1}{2}$  or 2 feet above low water level. Towards the shore cliff, the platform slopes slightly downward so that at the foot of the cliff it is approximately at low-water level. The limestone platform rises about 8 feet above this level. Between low-water and high-water level the cliff is strongly undercut, with the line of strongest erosion about at mean water level (Pl. viii, fig. 2). The overhanging ledge between mean and high water levels, or just about at high-water level, may be as much as seven or eight feet wide. This side of the island is exposed to the onrush of ocean waves, though, facing east, in the direction of the mainland, it does not have to stand up to the full forces of the ocean swell.

The west side of the limestone platform faces the lagoon side where wave action is very much less intense, although fair-sized waves may be set up by occasional north-westerly winds. On this side there is also a platform, approximately at low neap tide level, covered with calcareous algae of the *Lithothamnium* and *Lithophyllum* type and with *Vermetus* colonies. Along the shore there is, however, a high-water bench which is absent from the outer coast. This bench rises with a rather distinct step from the low-water level flat, and it slopes slightly upwards towards the foot of the cliff. Its position is at about mean high-water level and its surface is strongly pitted with solution holes. The limestone cliff rises about  $5\frac{1}{2}$  feet above this high-water bench and is only slightly or not at all undercut.

On both sides of the island the reef limestone forms a bare ledge between one and three or four yards wide. The remainder of the reef limestone platform is overlain by about 3 feet of shell limestone similar to that found on Little Island, but generally not so well stratified. The outcropping edge of this shell limestone is in most places concealed by accumulation of loose shells, mostly *Turbo* and *Trochus*, which are in an advanced state of weathering and can, therefore, not be of most recent age. Most of the shells have lost their prismatic layer and they must have been thrown onto the ledge when the sea stood higher than now.

From the edge of the shell limestone rises the outer beach ridge which, as has already been mentioned, forms a complete ring parallel to the edge of the platform. This beach ridge is 5 to  $6\frac{1}{2}$  feet high and rises to 13 feet above high-water level (Pl. viii, fig. 2; Pl. ix, figs. 2, 3). This is the oldest beach ridge on the island, formed at a time when all the rest of the island was still submerged. The shingle which constitutes this ridge is very strongly weathered and intensely blackened, and the composition of the accessory shell fauna is distinctly different from that of any other beach ridges observed. Also, in spite of its proximity to the coast line, it has an almost continuous cover of vegetation.

There are more mollusc shells mixed up with the coral shingle of this beach ridge than in any other beach ridge observed on the island. On the west side, shells of *Tridacna* up to 20 cm. long are quite numerous, whereas they are extremely rare on other beach ridges. Living *Tridacna* is also rare, only one living individual having been seen in this vicinity. Other common molluscs of the outside ridge are bailer shells (*Melo amphora*) of small to medium size and giant *Megalatractus arcuarius*. Furthermore, *Turbo* and *Trochus* are predominant, but *Patella* is also quite common whereas that genus does not now seem to live along this coast and is also rarely seen in other beach ridge systems.

Inside the ring formed by the outer beach ridge there is an area which has been completely disturbed by human action. Once guano deposits were found here, though now the surface of the shell limestone is exposed in some places and coral shingle and shells have been heaped up in others. The fossil fauna of these disturbed deposits is apparently similar to that of the outer beach ridge with large *Megalatractus* and *Patella* shells very much in evidence.

A small amount of rock phosphate must once have been formed in this place by alteration of some of the shingle underlying the guano, but phosphatization does not seem to have affected the shell limestone anywhere.

North of this raised limestone platform, the island widens considerably, which is due to the existence, about 400 yards to the north-west, of another raised limestone outcrop. Between these two raised limestone cliffs and in their "shadow", considerable deposits of shells, sand and shingle have been built by the combined action of the waters of the lagoon and of the open ocean. Coquina and shell sand deposits were built up from the lagoon side, coral shingle ridges from the outer side of the island.

From the north-western corner of the limestone platform which has been described above, the coast swings into a WNW. direction, and after about 300 yards of sandy beach, there begins another high-water level limestone bench, very similar to that along the lagoon side of the raised limestone platform in the south. It rises in a distinct step from the tidal (low-water level) flat occupying a position about 1½ feet above the latter (Pl. xii, fig. 3). It consists of reef limestone and its surface is fairly flat and strongly weathered by deep solution holes. It disappears inland under the cover of a shell bank, except near its southern end, where it is overlain by three feet of shell limestone. This shell limestone resembles that found on top of the raised reef limestone of Little Island and of the southern platform of Pelsart Island, although it occurs at a level at least five feet lower. There is only a small exposure of this shell limestone along the beach, but the limestone continues inland under a cover of shell and shell sand deposits. Its exact extent could not be determined, but it reappears in a small quarry immediately south of the workers' settlement around Trigg's Hut and from there it can be followed eastward to the guano field where it forms the basement rock of the guano and rock phosphate deposits. This limestone contains a fauna of small-sized molluscs, mostly gastropods of the *Coriella* type, and a few coral fragments. It is definitely not a rock laid down by the open ocean on the outer coast. It has the features of a lagoon deposit, but its fauna is unlike that of the lagoon shore of the present day.

Between this concealed limestone "island" and the southern platform, the island is made up of shell deposits of two different kinds. Immediately overlying the limestone are coquina beds and shell grits composed of small-sized pelecypods which are lined along the lagoon side by old beach deposits of larger shells, mostly *Turbo* and *Trochus*, mixed with a certain amount of coral fragments (see Saville-Kent, 1897, pl. xxvi); these beach deposits rise from sea-level in three distinct terraces, 3, 5, and 6½ feet above high-water level. Whereas the material of the first terrace looks fairly fresh, that of the second and third terraces shows slight surface blackening. Nowhere else on the island have accumulations of such large shells and coarse shingle been observed on the lagoon side.

The outer coast of the island north of the southern platform is formed by a series of shingle ridges in which coral fragments are very predominant, occasionally almost to the exclusion of other material. In the south, these beach ridges abut against the northern margin of the southern limestone platform. From there a well-developed

system of ridges can be followed for about 1,400 yards northwards to a place where the island becomes very narrow (Pl. ix, fig. 4). It is along this stretch that all important features of coral shingle beach ridges, as described in a previous section of this paper, can be studied in desirable detail.

The outermost beach ridge rises to between 5 and 6 feet above high-water level, but there is little doubt that this is an older ridge which is at present being worn down by the waves. It has a slightly grey surface and breaks off in a steep edge on the seaward side (Pl. xii, figs. 1, 2). Some of its material is undoubtedly now being reclaimed by the sea and is probably transported along the shore and partly redeposited in the beach ridge which is now under formation along the next section of the coast.

Landward from this outer ridge there is a series of subparallel ridges which sometimes branch or anastomose. It seems, however, from observations where the coast is straight and conditions have been uniform, that at least four major beach ridges or beach ridge systems are present. The ridges immediately behind the outer ridge are either of the same height as the latter or even sometimes slightly lower, but the inner ridges invariably rise to slightly greater heights. North-east of the workers' settlement the following heights of ridges were determined:

First ridge	.. .. .	..	5.5	feet	above	H.W.L.
Second ridge (a system of minor ridges)	..	3.0 to 6.0	„	„	„	
Third ridge	.. .. .	..	5.25	„	„	„
Fourth ridge	.. .. .	..	9.0	„	„	„

Although no statistical survey of the contents of the various beach ridges could be made, it is evident that there are distinct differences in their fauna. This could also be corroborated by observations in other parts of the island. Thus among the corals, *Platygyra* and *Favites* are quite common on the older ridges, whereas they are subordinate or even mostly absent from the younger ones. On the other hand, the number of specimens of *Turbo* and *Trochus* shows a distinct increase from the older to the younger ridges.

Between these beach ridge systems and the limestone in the west there is a flat depression in the surface of the island, undoubtedly the site of an old lagoon, now partly taken up by a swamp which, however, dries out in summer time. The bottom of this lagoon was covered partly by a thin shingle deposit, partly by shell sand, and must have served as nesting ground for large numbers of birds, probably the same species of terns which are still nesting there in large numbers, and which were responsible for the accumulation of many thousand tons of guano deposits in this depression and along its margins. Guano was also formed on higher ground, overlying the raised shell limestone to the west. However, it has been removed from there long ago and its relations to the other rocks are unknown. Where the guano accumulated on coral shingle the latter was cemented together and more or less completely phosphatized. Quantities of such rock phosphate must have been removed from the island in the past, for in the beginning of 1944 only a few hundred tons of this material were left.

At the bottom of the depression, the guano is underlain by a somewhat brittle phosphate rock which contains casts of many small gastropods of the *Coxiella* type. Such gastropods are elsewhere characteristic of lagoon conditions and the deposit is probably a completely altered lagoon shell sand.

Towards the north, the guano grades into guano-bearing shell sand of no commercial value and finally into pure shell sand and shell beds.

These shell beds have accumulated in considerable width in the western half of the island near the settlement and north of it. Immediately north of the limestone outcrops south of the settlement, and for some distance along the western coast, the deposit is of the pure coquina type with hardly any admixture of gritty or sandy material, but eastwards the shell beds are interbedded with shell grit and even with coral shingle layers. Towards the north-east and north, the material becomes gradually finer and can be described as shell sand. All these deposits form a flat surface about 6 feet above H.W.L. which is thoroughly undermined by the burrows of mutton-birds. None of the species of this shell deposit was found on the tidal flat and they must be washed up from deeper zones, below low-water level.

The supply of shells must be rather considerable, for there is rapid transport of material along the shore, and where obstacles are placed in their way, rapid accumulation of the shells takes place. Thus at the foot of a newly-built jetty a solid shell deposit accumulated in the course of three months, forming a rectangular triangle with sides 15 feet long, the deposit being at least  $1\frac{1}{2}$  feet thick. The tidal current along this part of the coast is particularly strong, because large quantities of water are constantly being brought across the half-submerged reef in the south into the lagoon and are pressed northward against the south-west coast of Pelsart Island. It is, therefore, easy to understand that lagoonal deposits of a coarse type have accumulated in large quantities in lee of the raised limestone outcrops which must once have formed islands.

About one mile from its southern end, Pelsart Island narrows rather abruptly and the character of the island changes completely. Near the outer shore all the older beach ridges terminate and only the outermost beach ridge continues unbroken. On the lagoon side it is lined by a narrow belt of shell sand deposit, and on its outer side, a fresh beach ridge is being formed at the present time which extends northward for another 1,200 yards. This is the coast of Batavia Road where ships may anchor in comparative safety a short distance from the shore. The low-water level platform narrows here considerably, and deep water (16 to 17 fathoms) is reached a short distance from the shore. There is no doubt that a strong current sweeps along the southern part of the coast and that this current supplies most of the material which is now being redeposited in more sheltered positions along the inner parts of Batavia Road.

The new beach ridge has been built up to a height of 4 to 5 feet and consists of rounded, white coral fragments. Behind it is a narrow lagoon, usually not more than 100 feet wide, with a sandy bottom. The lagoon is connected with the sea by several breaks in the beach ridge and is filled with sea water at every high tide. Landwards it is bordered by a slightly blackened ridge which forms the continuation of the outer beach ridge further south.

The narrow part of the island, where the new beach ridge begins, must be rather young. As has been said, all the older beach ridges cut out and it is probable that a gap existed here some hundred or hundred and fifty years ago. North of this narrow part, the island widens again to about 700 feet, older beach ridges reappear, and a new type of rock is now found along the west coast of the island. This is the shingle limestone whose general features have already been described earlier in this paper (Pl. xi). It is well exposed along the lagoon shore for about a mile where it forms a rock ledge varying in height from about high-water level springs to approximately 2 feet above this level. It rests on reef limestone which is found at varying levels between mean water level and high-water level springs. The shingle limestone is between 3 and 4 feet thick and usually bedded. As has already been described, it consists of rolled fragments of branching types of *Acropora*, and partly of larger flat colonies arranged in the characteristic roof-tile fashion of the deposits of the surf zone. The limestone dips  $5-10^{\circ}$ E., which is probably an initial dip owing to deposition on a sloping surface and the orientation of the roof-tile shingle shows that the deposit has been built up by waves from the direction of the outer coast.

The shingle limestone is overlain by beach ridges of the outer coast type.\* The break between the shingle limestone and the beach ridge shingle is always sharp, indicating that the shingle limestone must have been consolidated at the time of the formation of the beach ridges.

About a thousand yards further north the island narrows again to a width of about 150 feet. Here the new beach ridge along the outer coast terminates in an abrupt bend towards the coast. Also, the older beach ridges cut out and only one comparatively young ridge continues. North of this narrow portion the island again acquired a somewhat different character.

### (3). *Central Pelsart Island.*

This portion of Pelsart Island is characterized by the formation of sand spits and lagoons which provide a suitable environment for mangrove growth. The first of these

\* It will be shown later that beach ridges can also accumulate along the lagoon shore by the action of lagoon water, but their characteristics are different.

features is a string of three small lakes almost completely surrounded by mangrove in which large numbers of Lesser Noddies, a rare species of tern, *Megalopterus tenuirostris melanops*, are found nesting. These lakes might suitably be known as *Lesser Noddy Lakes* (Pl. xiii, fig. 1).

The mangrove patches here, as well as farther north in the vicinity of Mangrove Bay, must have been well established for several centuries, for they are shown on Jan Stejns' map of 1727 (see Heeres, 1899, p. 93) as places where firewood ("cromhout") was obtained.

South of the lakes, there is a little swamp with a sink hole in the middle in which the basal reef limestone of the island is exposed, probably approximately at mean water level.

The lakes, or rather the sand bars enclosing them, owe their existence to the fact that in this vicinity shingle limestone is outcropping along the outer coast. This shingle limestone forms a narrow ridge, not more than 100 to 150 feet wide, which is crowned by one comparatively youthful beach ridge. In the protection of this limestone ridge fine shell sand has been accumulated on the lagoon side. That these lakes and their sand bars might be a comparatively young feature is indicated by Adrian de Graaff's map of 1727 (see Heeres, 1899, p. 95), which shows in this vicinity a long narrow sand spit with an open lagoon behind it.

The mangroves here mostly grow on dry land and only rarely spread below high-water level. This is due to the proximity of the solid limestone base which is exposed at or slightly below low-water level. This low-water level flat is covered by a dense growth of *Lithothamnium* and *Vermetus* colonies. Also solitary specimens of *Megala-tractus* are found here; this is possibly the only place where this giant gastropod now lives in the vicinity of the island.

North of the Lesser Noddy Lakes, the island again narrows to a width of little over 100 feet. The island consists here of two youthful beach ridges, one of them crowned by an osprey's nest which forms an outstanding landmark in this low country. Along the outer coast there are occasional outcrops of shingle limestone. It is obvious that in this vicinity much of the shingle limestone had been removed by erosion before the shingle beach ridges were formed.

Approximately one mile farther north, the island swings definitely into a north-easterly direction which it retains until its northern end. Immediately north-east of the bend the southern end of Mangrove Bay is reached, a name which I propose to give to an inlet formed by two peninsulas projecting from the lagoon side of the island. These two peninsulas consist of shingle limestone, 3 to 5 feet thick, overlain by low shingle beach ridges of the outer coast type. The tip of the southern peninsula is connected with the main island by a sandbar, partly submerged at high tide, which at low tide bars the southern part of the bay.

The part of the island which separates Mangrove Bay from the outer ocean consists of one continuous outer beach ridge and a large number of short older beach ridges which are arranged vertical to the longitudinal extent of the island. There is evidence here that prior to the formation of these ridges the site of Mangrove Bay was an open passage between the lagoon and the ocean, which was gradually closed by beach ridges oriented more or less parallel to the shores of that passage. From their weathering and blackening it can be seen that the ridges in the middle of the bar separating Mangrove Bay from the ocean are younger than those at either end.

North-east of Mangrove Bay, the island widens slightly and consists of a series of beach ridges which increase regularly in age and in height from the outer to the inner coast (Pl. vii, fig. 2). The lagoon coast is here formed by reef limestone which reaches to about one or two feet above high-water level where it forms a narrow ledge. It is overlain by one or two feet of shingle limestone on which rises a very old beach ridge to a height of about 10 feet. From here the height of successive beach ridges decreases gradually to five or six feet in the outermost beach ridge along the coast. Unfortunately I had no facilities for taking accurate levels for which this locality would be ideally suited, because it demonstrates so very clearly the part that emergence of the island has played in the formation of the beach ridge systems.

About half a mile further on, the old beach ridges begin to swing towards the lagoon shore where they terminate. We are approaching the narrowest portion of the whole island, the site of another gap which can only have been closed in comparatively recent times.

It is important to notice that along its entire length the outer coast of the central part of Pelsart Island, which has just been considered, is being degraded in much the same way as has been described for the beach ridge coast south of Batavia Road, in the southern part of the island. All along the central part of the island the outer coast is formed by a continuous beach ridge with a little weathered, but slightly greyish, surface which breaks off in a steep cliff against the sea. There is no doubt that this ridge is now for its entire length eroded by the waves and that shingle material is taken from it, transported along the coast and redeposited at the northern end of the island.

#### (4). *Northern Pelsart Island.*

It has been said above that as we approach the northern part of the island, the older beach ridges north of Mangrove Bay swing towards the lagoon shore and terminate there. They are followed by a series of somewhat younger ridges that run obliquely across the ever-narrowing island between the two outer beach ridges and the lagoon shore. Finally, these oblique ridges as well as the innermost of the two outer ridges disappear, and for a distance of 400 yards the island consists of only one shingle ridge, lined on the lagoon side by some sandy sediment on which a narrow fringe of mangrove grows. It seems that this is the site of another comparatively recent gap in the island, a gap which, however, had already been closed when the island was investigated by the *Zeeuyck* crew in 1727.

From the northern side of the old gap to the northern tip of the island, the structure of the island is again different from that of any other part. As usual, there is, of course, an outer beach ridge, but inside this is a series of ridges that run across the island oblique to its longitudinal axis, approximately at an angle of  $45^\circ$ . This system of oblique ridges is only interrupted in one place, about 500 yards from the northern end of the island, where a few younger longitudinal ridges indicate the presence of an old gap, perhaps caused by a short break-through of the sea. Finally, all along the lagoon coast there is another longitudinal beach ridge which consists of coral shingle which is finer and more rounded than the shingle of ordinary beach ridges. This beach ridge rests unconformably on the oblique ridges and there is no doubt that it has been formed by the action of the waves of the lagoon side after the oblique ridge system had been built. The material of this inner beach ridge might be derived partly from the erosion of the oblique ridges, but some of it is so well rounded and of such small size that it looks as if it comes from the destruction of shingle limestone which is absent from this part of the island except for two small erosion remnants near the northern end.

The arrangement of the beach ridges shows that all along, this part of the island has grown in a north-easterly direction by the deposition of shingle material by shore currents which swept around its north-eastern end. These same processes are still in operation near the northern tip of the island. Towards the north the beach ridges become obviously younger, as may be expected, and the northern bulge of the island consists of beach ridges which are little weathered, only slightly blackened and almost bare of vegetation. About 500 yards from the north end of the island there is a change in the nature of the processes active along the coast. The outer beach ridge which is being degraded all along the coast farther south turns away from the coast, runs obliquely across the island and terminates against the lagoon shore. A succession of younger ridges has been formed on its outer side, the youngest of which reaches as far as the northern tip of the island and is still in the process of formation. In other words, aggradation of the coast takes place here.

The coral fragments of which these newer ridges are composed are all very strongly rounded and worn down, which seems to indicate that they may be mostly material derived from the coastal beach ridge further south which has been transported for varying distances along the coast.



The island is still pushing on in a north-easterly direction towards two small islets which are situated a few hundred yards from its northern end. These islets consist of raised limestone whose nature could not be ascertained from the distance. In time they will become parts of Pelsart Island.

Situated on the north-west side of the northern part of Pelsart Island is an area of strong coral growth, the "maze" which has been briefly described by Dakin (1919, p. 173). The edge of the "maze" can be clearly seen even at high water when the corals are completely submerged, but I had no facilities for studying this interesting part of the lagoon. An abundance of coral growth in this area was already noticed by members of the crew of the *Zeeuwycck*, in 1727, for it is noted on Jan Stejns' map that corals occur here in "bosjes" (bunches).

(5). *The Outer Reef of the Pelsart Group.*

As has been shown, Pelsart Island is built on a foundation of coral reef limestone which forms a platform at approximately low-water level and above which rise a few erosion remnants indicating an earlier, higher, position of the reef. Pelsart Island continues southward into a reef which is slightly submerged at high tide (Pl. viii, fig. 1). This reef trends at first south-westwards for about a mile, then swings around into a north-westerly direction in which it continues for over ten miles until it ends in a large eastward-pointing hook at its northern end. The width of that part of the reef, which is regularly exposed at low tide, varies from about 100 yards to almost a mile, and in general it is much wider in its northern half than near the southern end.

In January, 1944, part of the surface of the reef was exposed at almost every low tide. The highest elevation of the reef surface above the water level of the lagoon side actually measured during this period was 1 foot 10 inches (Pl. x, fig. 2). The outside of the reef is exposed to the full force of the breakers of the Indian Ocean and the reef, therefore, can only be examined when no high swell is running.

In its southern part, the only portion which I have been able to study, the reef is composed of two parts:

- (1). An outer rim which becomes exposed at low tide and which on the average is about 100 yards wide, but in places narrows to 10 or 20 yards.
- (2). An inner platform, on the average perhaps 3 to 5 feet below the level of the outer rim, and sloping gradually towards the lagoon, but whose inner edge I have not been able to study.

The *outer rim* corresponds rather closely to the picture that Marshall (1931) has given of the *Lithothamnium* rim of his "rough water" type of coral reefs. Seen from a distance, its surface appears smooth and perfectly flat. On closer inspection, it is found that the top of the reef is completely encrusted with limestone deposited by calcareous algae which forms a slightly uneven and somewhat slippery surface. This surface is remarkably monotonous and almost uninhabited by other forms of life, except around the southern bend of the reef. Near Little Island, the surface of the reef is pitted by innumerable holes each occupied by an echinoid, *Echinometra Matthaei*, in a manner which has so often been described from coral reefs. Also, specimens of *Turbo* and *Trochus* are fairly numerous in this vicinity, but apart from these three species, very few animals are found on top of the reef. Below the surface, however, there is considerable activity of boring organisms, mainly pelecypods and annelids, which undermine the algal limestone crust in places to such an extent that one breaks easily through when walking over it.

In the vicinity of the southern bend of the reef there are also numerous depressions in the surface in which pools form during low tide. Coral colonies can be found in all of these pools, though usually not in great numbers.

The effect of the position of the water level on coral growth is most marked in these pools, for in species which tend to grow in more or less spherical bodies such as *Platygyra lamellina*, *Favia* and *Euphyllia*, the colonies are cut off sharply just below the water level of the pool and have a flat dirty surface on which some sediment accumulates and to which water plants are attached. Wood-Jones has figured and described

specimens of a very similar shape from the Cocos-Keeling atolls and attributed their deformation to the stoppage of the growth of the upward-directed polyps owing to the accumulation of excessive sediment on top of the colony, but this explanation cannot apply in the case of the similarly shaped coral colonies in the pools of the Pelsart Reef, where their growth is clearly interrupted by the fact that they have reached the water level of the pool.

The outer edge of the rim is indented by channels (Pl. x, fig. 1) which are, on the average, six to ten feet wide and of very varying length though mostly not less than 30 feet long. Through these channels the water surges outward with great force between two breakers, and there is no doubt that they are being kept open partly by erosion and partly by the inhibition of coral and algal growth by the continuous strong currents which are set up in these channels. It has been pointed out by Krämer (1927) that such channels are apparently normal features of the outer edges of barrier reefs and that they may be compared to the inlets of tidal flats of low sandy coasts, particularly as found along the shores of the North Sea. However, such tidal inlets are created and kept open by tidal currents rather than by wave action.

On the surface of the outer rim are found negroheads,\* which occur in great number on the reef between Little Island and the southern bend of the reef (Pl. viii, fig. 1). Most of these are rather small blocks of coral limestone, not more than about two feet in diameter. They rest loosely on the surface of the reef and are probably still being shifted by the waves during major storms, so that they have no time to become cemented to the reef. Small negroheads can be found on the tidal flat along the west coast of Pelsart Island at a distance of as much as 400 to 500 yards from the outer edge of the reef.

The most interesting negroheads are found about two miles from Little Island and not far from the wreck of the *Windsor* (Pl. x, fig. 3). Here, a large block of coral limestone, about four feet high and six feet long, rests on the level surface of the reef. Against it leans another large block of almost equal size. The former block is firmly cemented to the reef and seems to form part of it, so that one could easily derive the impression that it is an erosion remnant, indicating that the reef once stood at a general higher level. This, of course, was Agassiz's explanation of negroheads which has been refuted by most other observers on coral reefs. Owing to the late hour of the morning and the rapidly incoming tide, this occurrence could not be studied in desirable detail. However, it seemed that this limestone had very much the same appearance as that of the elevated platforms of Little Island and Southern Pelsart Island, with the corals, mostly branching *Acropora* colonies, in their original vertical position. Further along the reef there seemed to be additional negroheads of large size which it might be worthwhile to include in future investigations.

In view of the fact that, as Umbgrove (1931) and Kuenen (1933) showed in the East Indies, very large negroheads, that is, coral limestone blocks of several tons' weight,† are only found in areas occasionally visited by hurricanes, the presence of such blocks on the Pelsart Reef seems puzzling, for the Abrolhos Islands are well outside the hurricane zone. It is, therefore, most likely that these, and similar limestone blocks that can be seen on the reef further along, are erosion remnants indicating a former higher reef level which, however, on the exposed western side of the Pelsart Group has been levelled down almost completely.

\* The term "negro head" was introduced by Flinders (1814, Vol. ii, p. 88) for boulders of coral limestone which were "blackened by weather" and stood higher than the rest of the reef, "the forms of the different corals, and some shells" being distinguishable in them. There has been a tendency among later writers to change the term to "nigger heads", but the perpetuation of this term in scientific literature cannot be recommended.

† As used by Umbgrove, Kuenen, and many others, the term "negrohead" should be restricted to coral limestone blocks of very large size, but it is doubtful if any justification for this usage can be found in Flinders' writings. He refers to them first on p. 83 of his work (1814, Vol. ii) as "small black lumps, which at a distance resemble the round heads of negroes". On p. 85 he mentions their irregular distribution on the reefs and observes that they are nearly all covered at high water. It seems that Flinders included in this term coral boulders and limestone boulders of any size.

(6). *Geological History of Pelsart Island.*

The site of the present Pelsart Island was originally occupied by a coral reef in which Acroporidae were by far the most abundant forms. The growth of this reef was then interrupted, and 2 to 4 feet of shell limestone were deposited on top of the reef. The surface of the reef was probably irregular and the layer of shell limestone followed more or less the irregularities of the reef top.

The reef with its cover of shell limestone then emerged by at least six, probably eight, feet and much of the part above sea-level was destroyed by marine erosion. A few erosion remnants were left standing in the southern part of the island.

Following this period, the reef was again submerged to such an extent that subaqueous shingle deposits, later cemented into shingle limestone, could accumulate on the eroded parts of the reef. Also, during this period the oldest beach ridges accumulated on those parts that had been saved from erosion. The fact that the fauna of these oldest beach ridges differs somewhat from that of the present day indicates slightly different conditions, though it is as yet difficult to give an idea of the nature of these differences. Both the accumulation of subaqueous shingle deposits and of coral shingle beach ridges indicate that reef-building corals were now again growing vigorously in the waters alongside the old reef.

Some time later the reef emerged slowly, part of the shingle limestone was eroded away and a series of beach ridges was formed on the slowly emerging platform. The oldest of these now rise to about 11 feet above sea-level and were probably formed when the sea-level stood at least 5 feet higher than now. The formation of the oldest beach ridges of this cycle began simultaneously in several places and the island grew gradually by the joining up of older shingle islands by younger ridges. In the beginning, this process was occasionally interrupted by storm floods creating gaps in the shingle ridges which then were closed by new ridges, and it is fairly certain that Pelsart Island acquired its present shape not more than a few hundred years ago.

While shingle deposits were thus heaped up from the outer side of the island a certain amount of aggradation also went along the inner side in the form of deposition of shell and shell sand deposits and in places even of shingle ridges.

During the most recent period of its history, the island has been growing mainly by addition of shingle ridge deposits at its north-eastern end and this process is in operation to-day.

At present the emergence of the island seems to have come to an end and the sea-level is either stationary or perhaps even slightly rising. The outermost beach ridge which lines the east coast of the island, and which was formed probably not less than 100 years ago, is now being degraded along almost the entire length of the island. Accumulation of new beach ridge material takes place only along a short stretch of coast on Batavia Road, and near the north-eastern extremity of the island.

## EAST WALLABY ISLAND.

East Wallaby Island (Fig. 2) consists of two morphologically different parts. The western half is a low limestone platform, the edges of which are largely concealed under a cover of dunes and which is surrounded by sandy beaches. The eastern half is hilly, rising to almost 50 feet above sea-level, and for its greater length breaks off in a low cliff towards the sea. A north-eastern promontory, Fish Point, projects into the sea, and on the western side of this peninsula, on the shores of Turtle Bay, one of the most impressive emerged coral reefs of the Abrolhos Islands is found.

(1). *The Western Limestone Platform.*

The western limestone platform occupies much of the western and central part of the island. Its height is about 8 to 10 feet above high-water level. The base of it is reef limestone whose surface is on the average about 2 feet above high-water level. This is overlain by 6 to 8 feet of shell limestone which is exposed in a few places in coastal cliffs and in three or four sink holes in the middle of the platform. In the westernmost of these holes (marked as "Well" on the Admiralty Chart) it can be seen that the uppermost 2½ feet are shell limestone with various shells of small size as well as some

*Vermetus* specimens. Below this layer, down to 6 feet, is massive limestone with large shells and coral fragments. The upper limestone gives the impression of having been formed under conditions similar to those now prevailing along the south-eastern and southern shores of the island, whereas the lower limestone was evidently formed under different conditions, probably at a time when there was still some active coral growth in the vicinity of the island.

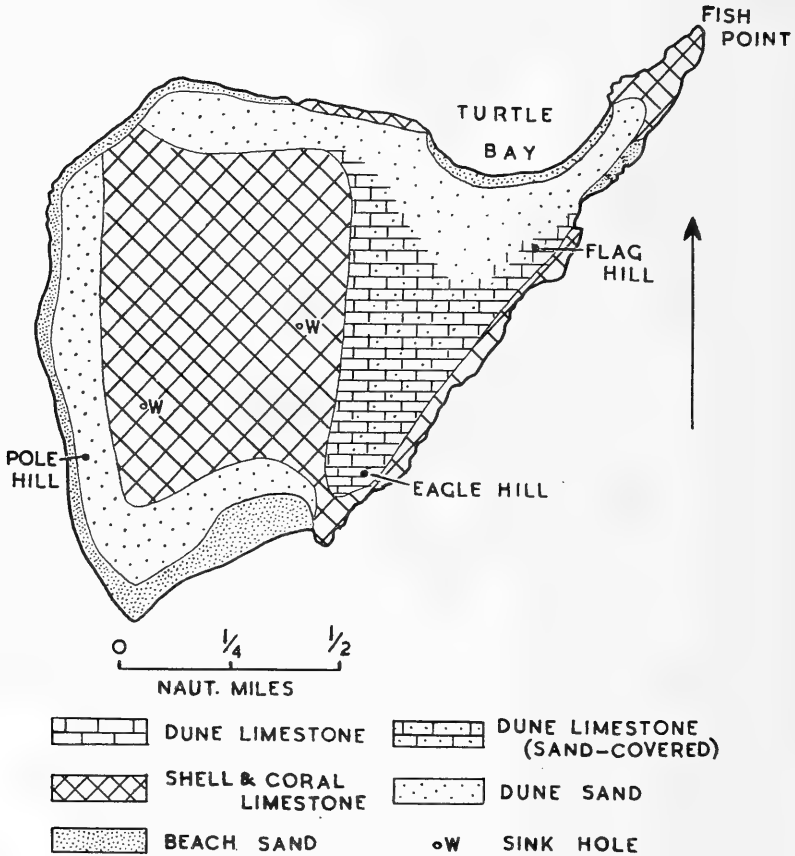


Fig. 2.—Geological sketch map of East Wallaby Island. (Topographic base adapted from British Admiralty Chart 1723.)

In the easternmost sinkhole (also marked "Well" on the Admiralty Chart) the water level was found to be 8 feet below the surface, and although the bottom of the hole was inaccessible, it looked as if the basal reef limestone was exposed a foot or so above the water level.

The limestone breaks superficially into slabs of irregular size (Pl. xiii, fig. 2).

In many places, a brittle, light grey calcareous deposit was found on top of the limestone which contains small gastropods of the *Coxiella* type and other small shells. This is undoubtedly a dried and somewhat solidified calcareous ooze of the same type, to be described later, that is now under formation on the tidal flat off the Wallaby Islands.

Everywhere on the limestone platform there are scattered fragments of very strongly weathered corals such as *Acropora* and *Favites*, also occasional bailer shells (*Melo amphora*), *Vermetus*, and other shells, but there is nothing like a continuous shingle cover, large patches of the limestone surface being entirely free from any coral or shell

fragments (Pl. xiii, fig. 2). Such fragments as are present show evidence of great age. They are at least as strongly weathered and blackened as the oldest coral shingle on Pelsart Island.

Around the edge of the platform there is a fringe of low dunes which, in Pole Hill on the west coast, rise to a height of 40 feet, but are usually lower, their average height not exceeding 20-25 feet.

(2). *The Eastern Half of the Island.*

Towards the east the limestone platform disappears under a cover of dune limestone, but good exposures along the shores show that it continues unchanged as far as Fish Point, the north-eastern extremity of the island. Along the coast, south of Fish Point, the cliff stands about 8 feet above the low-water level platform, and at least five feet above high-water level. Over most of the north-eastern part of the island, with the exception of the vicinity of Fish Point, this coral and shell limestone is overlain by younger deposits, mostly of dune limestone.

The dune limestone can be best studied along the south-eastern side of this part of the island, where it reaches its greatest thickness at Flag Hill. Here the section is as follows:

Basal limestone	.. . . . .	5 feet
Dune limestone	.. . . . .	26 "
Recent sand dune	.. . . . .	16 "

Further south at Eagle Hill, the dune limestone is 22 feet thick. Its surface is strongly undulating, as can be seen particularly well when approaching the island from the east.

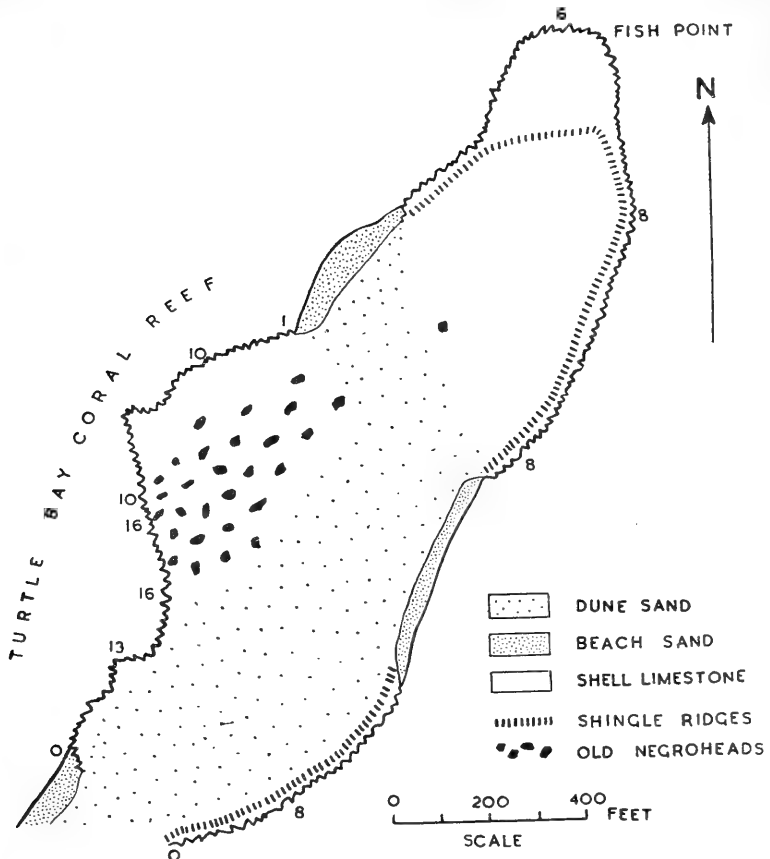


Fig. 3.—Geological sketch map of the north-eastern promontory of East Wallaby Island. The figures indicate height above H.W.L. of edge of limestone platform.

In some places between Eagle Hill and Flag Hill the thickness is reduced to a few feet. The undulating surface of the limestone suggests an ancient dune landscape. The limestone is not well exposed along the slopes, but the characteristic root structures are well seen in a number of places.

Covering the dune limestone are calcareous sand dunes of more recent age which at Eagle Hill and at Flag Hill rise to 16 feet above the surface of the dune limestone. They are covered by rather dense vegetation and seem to be more or less fixed. It is doubtful whether much addition of sandy material takes place at the present time. This dune sand is now being cemented a short distance below the surface and forms a brittle, yellowish rock which in some places stands out in little pinnacles above the surface of the dune, where the loose sand has been removed by the wind. Where exposed at the surface this cemented dune sand is strongly cavernous.

It seems that most of the surface of the north-eastern portion of East Wallaby Island is formed by dune sand which overlies dune limestone, with the exception of the north-eastern extremity of the island near Fish Point, as has already been mentioned. This is the only place where a shingle beach ridge has been observed on the island (Fig. 3). It emerges beneath a cover of dune sand 170 yards south of Fish Point, follows the edge of the cliff for a short distance and then crosses to the other side of the peninsula, where it again disappears under a sand cover. This shingle ridge consists of very strongly weathered and blackened coral fragments with an admixture of shells, mostly of *Turbo* and *Trochus*.

In the middle of the Peninsula, 230 yards SW. of Fish Point, a huge boulder of coral limestone, about 4 feet high, rests on the limestone platform. This is an old "negro-head" which has been thrown onto the limestone platform when the latter stood at approximately high-water level. On it an osprey has built a nest to the height of 8 feet above the ground, thus providing a landmark which must be visible from far out to sea.

Many more such boulders, though mostly smaller, are found further south along the north-west coast of the peninsula, on top of a large dome-shaped reef structure which deserves some closer attention.

### (3). *The Turtle Bay Reef.*

When approaching Fish Point from the south-west, along the shore of Turtle Bay, the eye is at once arrested by an uparching of the surface of the limestone platform along the northern half of the coast of this bay (Pl. xiv, fig. 1). This is a raised coral reef which must once have been more or less circular in outline and half of which has been removed by erosion after emergence.

Measured in a straight line from north-east to south-west the diameter of the reef is 330 yards. When approached from the south its surface is seen to rise from underneath the sandy beach which forms the greater part of the shore of Turtle Bay, first quickly, then more slowly, to a maximum height of about 16 feet above high-water level, which is sustained for some distance along the middle part of the reef. On the northern side the surface slopes down gradually until it disappears beneath beach sand.

The core of the dome structure is occupied by coral reef limestone. Near the edge of the reef there is less *in situ* growth of corals in evidence and the limestone consists mostly of broken fragments and shell débris with shells of pelecypods and of *Turbo*. However, towards the centre the coral growth becomes more luxuriant and the number of shells in the limestone decreases. Near the southern edge of the reef thick-branched

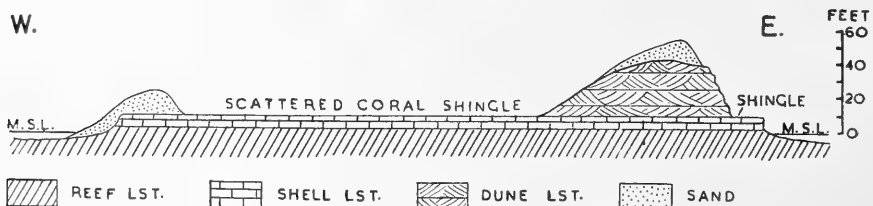


Fig. 4.—Geological cross-section of East Wallaby Island.

species of *Acropora* predominate. Approximately at the place where the surface of the reef stands at 8 feet above high-water level a foliose type of *Acropora* becomes more numerous (Pl. xiv, fig. 3). This species grew here in beautiful, large individuals, stacked one on top of the other like a pile of dishes. Interspersed are thick-branched colonies of *Acropora*, but also occasional massive colonies of *Platygyra lamellina* measuring as much as 3 feet across.

The cliff is undercut at about high-water level, in places to a depth of 10 feet.

Farther towards the centre of the reef, branched and foliose species of *Acropora* contribute to about equal degrees, but in addition to *Platygyra* colonies *Favites* and *Goniopora* now also appear as subordinate members of the fauna.

At the highest point in the centre of the dome the reef limestone is overlain by 5 feet of shell limestone so that the surface of the reef itself is here 11 feet above high-water level. Above the reef limestone lie  $2\frac{1}{2}$  feet of uncemented or loosely cemented shell and coral grit with occasional lenses of coral shingle. This deposit is indistinctly stratified. It is overlain by  $2\frac{1}{2}$  feet of more massive limestone consisting mostly of cemented shell grit with a fair number of entire shells, but hardly any coral fragments. This deposit becomes more fine-grained towards the top and passes into the fine-grained shell limestone of the type that is usually found at lower levels, overlying the basal reef limestone of the island at, or just above, high-water level.

The entire surface of this reef, as far as it is not covered by sand dunes, is strewn with boulders of various sizes, partly of shell limestone, partly of coral limestone, some measuring up to two cubic yards (Pl. xiv, fig. 2). In addition, there are a good many weathered and blackened coral specimens scattered over the surface and also loose shell fragments. All of this material—boulders, coral shingle and shells—must have been thrown onto the reef when this stood very much lower relative to sea-level, probably just when it began to emerge.

The Turtle Bay Reef is a puzzling feature in the geology of the Wallaby Islands. It is obviously of the same age as the reef limestone which forms the bulk of East Wallaby and West Wallaby Islands and which is nowhere found at a greater height than four or five feet above high-water level, that is, the upper surface of the coral formations in the Turtle Bay Reef rises at least six feet above any other ancient coral formation of these Islands. It will be shown later that the amount of emergence of the Turtle Bay Reef agrees best with that shown by the Dongarra Reef on the mainland coast, south of Geraldton. An interpretation of these facts will be attempted in a later section of this paper.

#### (4). *Some Coastal Features and the Submarine Platform.*

It has already been said that sand beaches are more predominant on East Wallaby Island than on any of the other islands. They form the south-eastern, south-western, western, and much of the northern coast of the island. Around the south-eastern corner of the island the beach deposits are rich in shells of gastropods and pelecypods. Except for *Melo*, *Trochus*, *Spondylus* and *Vermetus*, the beach assemblage consists predominantly of very small shells. Also, tests of the large foraminifer *Marginopora* are very important constituents of these sands.

The west and north coasts of the island are bordered by sand dunes which, on the west coast, rise to a maximum height of 40 feet; those on the north coast are lower.

Between East Wallaby Island and West Wallaby Island extends a submarine platform which is probably between one or two feet below low-water level springs, and which consists of coral reef limestone. It is covered with green algae, but otherwise there is surprisingly little life on it. In places, especially near the south-east corner of East Wallaby Island, there are numerous borings of a *Polydora*-like worm which penetrate the surface layer of the limestone. Here and there some alcyonarians lend a touch of colour to the dull surface of the platform and there are occasional colonies of *Vermetus* and some small patellids.

A large part of the surface of the platform is covered with a slimy calcareous mud which is probably the product of algal secretion. Algae form a thin green zone near the surface of this deposit. Deposits of this mud can be best studied near some small

islands which are situated half-way between East and West Wallaby where the deposit occurs in some thickness between and around them. In pockets of the reef limestone several inches of the mud may accumulate, but on flat surfaces it is usually one or two inches thick. Along the east shore of a long narrow isle which rises from the margin of the submarine platform, the mud passes gradually into shell grit and *Coxiella* deposits. In the marginal zone the mud breaks up into small mud cakes or mud pebbles, with irregular, rounded or angular outlines, rarely more than two inches in diameter. These are moved about by small waves and become embedded in the shell grit and *Coxiella* beds—a fine example of the formation of an intraformational conglomerate or breccia.

Formation of pure shell deposits, mostly composed almost entirely of *Coxiella*, is in progress in various places around these islands. There is usually very little admixture of other shells, and *Marginopora*, so prominent in the beach deposits of East Wallaby, is entirely absent. The islands themselves are limestone platforms about 5 feet above high-water level, which are covered with shell deposits whose composition is essentially the same as that of recent beach deposits in the vicinity. These shell deposits are now covered by dense scrub and must have been formed when the surface of the islands was near water level. It is significant that there are no coral shingle deposits on these small islands.

A few words may in this connection be said about the geology of *Pigeon Island* which is separated from the platform of the Wallaby Islands by a narrow stretch of somewhat deeper water which provides good anchorage for smaller vessels. Pigeon Island is a small limestone platform that rises to a height of 7 to 9 feet above high-water level. The reef limestone rises to 4 or 5 feet above high-water level, that is, higher than on most places on the Wallaby Islands. It is overlain by 2 to 4 feet of shell limestone. The island was once undoubtedly covered by shingle deposits and boulders (negroheads), mixed with and overlain by guano, but the original relations of the deposits have been strongly disturbed since the guano has now been entirely removed. Along the south-east coast of the island one can still see parts of an old shingle ridge on top of the cliff, separated from the edge of the cliff by a bare ledge about 3 to 4 feet wide. The beach ridge consists of very strongly weathered corals, some shells, and boulders of shell limestone.

#### WEST WALLABY ISLAND.

Like East Wallaby Island the greater part of West Wallaby Island is made up of, or underlain by, a platform of reef and shell limestone which rises 6 to 10 feet above high-water level. This limestone platform forms the north-east coast and the northern half of the east coast, and it is also exposed along the south coast and the southernmost part of the west coast. The outline of the platform is, however, much more irregular than that of the island which owes its present features to some extent to the effect of silting up of sand and shell deposits in the indentations and embayments of the platform. In the southern part of the island the limestone platform is overlain by dune limestones.

##### (1). *The Northern Part of West Wallaby Island.*

The north-east coast of the island, from the easternmost promontory to the northern tip, is formed by a limestone ridge, 100 to 200 feet wide, which forms a steep, undercut cliff on the outer (north-east) side, whereas it slopes gently on its inner (south-west) side, where the limestone disappears under a cover of shell sand. The foot of the outer cliff is only slightly above low-water level. It rises from a platform which close to the coast stands very little above low-water level, sloping gradually away from the shore to the general level (about 1 to 2 feet below low water) of the submarine platform which connects the two Wallaby Islands. In some places this coastal platform is sculptured by shallow erosion channels vertical to the coastline which are probably caused by backwash of the waves. Otherwise the surface is flat with the exception of lumps of dark-coloured limestone which are irregularly scattered over the flat. These have very cavernous, strongly-weathered surfaces and are the erosion remnants of larger lumps of greyish limestone, up to 2 and 3 feet in diameter, which are embedded in the



reef limestone of the platform. The dark-coloured limestone is rather homogeneous and contains occasional shell remains. Similar dark limestone lumps are also quite prominent along the east coast of the island. From a distance they look very much like negroheads on a reef. It is most likely that they are the fillings of pockets on the surface of the underlying reef limestone. When the latter was levelled down to its present position at and below low-water level, the homogeneous limestone fillings proved more resistant to erosion.

The profile of the overhanging cliff of the north-east coast is somewhat different from that observed elsewhere on this and on other islands (Pl. xvi, fig. 1). It is usual to find a deep erosion notch at about mean water level and a wide overhang, sometimes almost horizontal, just above high-water level springs. This cliff, however, has a profile which slopes evenly from the edge of the raised platform inwards towards the tidal platform. Just above the latter, the foot of the cliff is rounded and somewhat carved out, and from here erosion works in places deeply into the limestone. Whereas the normal overhang of the cliff is about 6 feet, just above the level of the tidal flat the limestone may be undermined by solution for a depth of 20 feet and perhaps more. This often results in the final collapse of the overhanging ledge owing to its own weight. In places where a considerable portion of the ledge has collapsed, silting up usually ensues and the coast is then protected from further erosion (Pl. xvi, fig. 2).

It should be noted that the features of this cliff coast can hardly be caused by mechanical action of the waves. The coast is well protected by the shallow submarine platform mentioned already and by outlying islands to the north and north-east. Moreover, it faces in a direction from which in that region wind seldom ever blows. From the way in which small trees are deformed on the island it can be seen that the predominant winds are approximately from the direction  $10^{\circ}$  E. of S., although in the winter regular north-west storms occur. Solution must, therefore, play an important part in the formation of this shore profile, but the matter cannot be followed up in more detail here.

Towards the northern end of the island, the outer cliff becomes slightly higher until it rises to about 9 feet above low-water level, that is, about 4 feet higher than farther south. This rise is almost entirely due to an increase in the thickness of the shell limestone. Along much of this part of the coast this shell limestone is rich in small gastropods, probably *Coxiella*.

The surface of the limestone ridge, which, as has been said, forms the north-east coast of the island, is strewn with scattered coral shingle and shell remains, all of which are strongly weathered and blackened. The inner side of the ridge has a gradual slope and is covered by many large boulders of reef and shell limestone which must have been thrown up by the sea. To the NW. it disappears under a cover of shell sand which contains shells of mostly small to moderate size. Its fauna is of very similar composition to that of the beach deposit around the south-east corner of East Wallaby Island, small gastropods, *Vermetus*, *Marginopora* and *Lithothamnium* being predominant. This sand forms a plain which occupies much of the western half of the northern end of the island, but it is hard to cross because it is completely undermined by the burrows of mutton-birds. In some bare patches on the surface, shells have been strongly concentrated as a deflation residual.

The limestone of the central part of the island, which reaches the coast in low cliffs south of the easternmost promontory of the island, is very monotonous. The cliff formed by it is everywhere 5 to 6 feet above low-water level, probably on the average not more than 3 feet above high-water mark, although the platform may rise somewhat towards the interior of the island. The cliff on the east side is generally more or less vertical with a shallow erosion channel near low-water level. There is very little overhang.

The reef limestone rises seldom above high-water level, the remainder of the cliff being formed by shell limestone.

The surface of the limestone platform is strongly weathered. Here, as on East Wallaby Island, the limestone is gradually broken up by numerous joints which run in all directions, no definite joint systems being discernible. Solution by rain water

proceeds along these joints, the limestone pieces between the joints are rounded off, and the surface begins to resemble a cobble pavement. The great age of this platform is also emphasized by the formation of initial rain rills on the sides of the "cobbles", a feature not observed elsewhere.

There is one sink hole with good water in this limestone platform, situated about 200 yards from the shore of the second bay south of the easternmost promontory of the island.

(2). *The Southern Part of West Wallaby Island.*

The best picture of the structure of the southern half of West Wallaby Island can be obtained in the region around its south-west corner. The south coast and the west coast for about one mile from the south-west corner form steep cliffs (Pl. xv, fig. 2). Particularly along the south coast there is strong erosion by the sea.

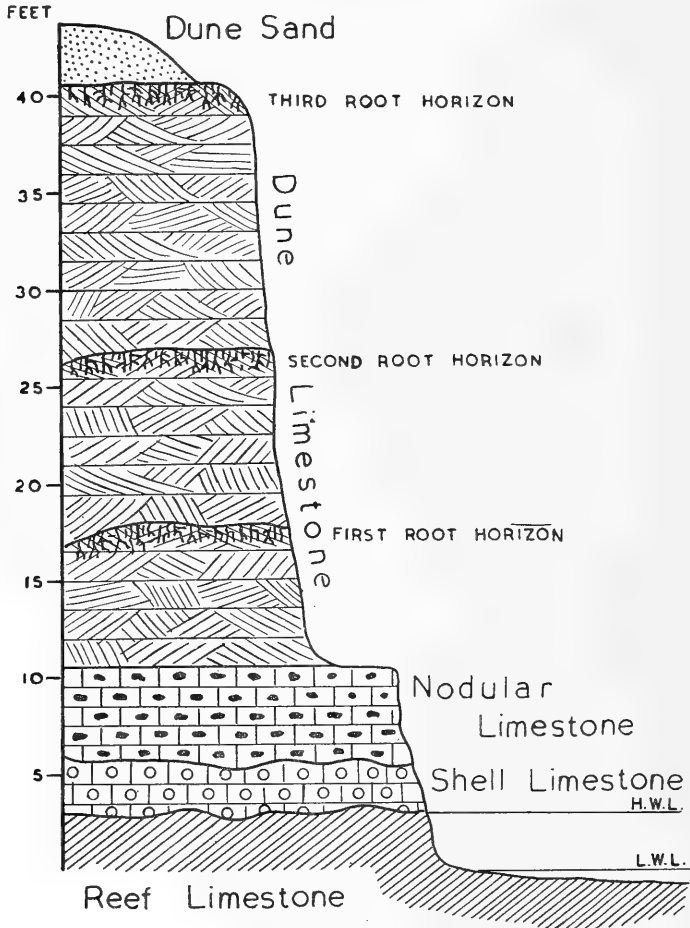


Fig. 5.—Geological section in the south-western part of West Wallaby Island.

Along the south coast and the southern part of the west coast, the base of the cliff is formed by reef limestone which, as a rule, does not rise above high-water level; only around the south-east corner of the island does the reef limestone reach about 1 foot above high-water level. It is overlain by shell limestone which is, as a rule, 3 to 4 feet thick. This is followed by a bed of limestone which weathers into nodules and contains occasional traces of root structures. This limestone is of varying thickness and forms a horizontal ledge along some parts of the coast. On top follows homogeneous dune lime-

stone, with root structures, which rises to the highest elevation (about 35 feet above sea-level) near the south-western corner of the island. The general geological section in the southern part of the island is, therefore, as follows (Fig. 5):

- |                         |  |               |
|-------------------------|--|---------------|
| 4. Dune limestone       | .. .. .                                | up to 30 feet |
| 3. Nodular limestone    | .. .. .                                | 1-7 "         |
| 2. Shell limestone      | .. .. .                                | 3-4 "         |
| 1. Coral reef limestone | from about high-water level downwards. |               |

The corals of the reef limestone weather out very well in places on the narrow tidal flat (Pl. xiv, fig. 4), and also around the south-east corner of the island. The shell limestone is very variable in its structure and composition. It may be fine-grained and homogeneous, but in places it is gritty and contains large shells or fragments of large shells. This limestone retains a fairly constant thickness and its surface is, therefore, more or less parallel to the major irregularities in the surface of the reef limestone. The nodular limestone more or less fills the depressions in the surface of the shell limestone and has itself a fairly plane and horizontal surface. The nodules are undoubtedly of secondary concretionary origin and are due to the deposition of calcium carbonate from solution. The absence of shells from this bed suggests subaerial origin. It represents perhaps wind-blown sand from the belt just inside the beach. On top of it rests, with a marked disconformity, the dune limestone. As on East Wallaby Island, its surface is undulating (Pl. xv, fig. 2). It forms a number of parallel ridges, undoubtedly old dunes, which cross the island in a general north-westerly direction from the south coast towards the west coast. They are now being strongly eroded along both coasts. On the average, they rise to little more than 20 feet above the surface of the nodular limestone. Root structures are visible in this limestone almost everywhere, but outcrops are usually not good. In one place on the south coast two very distinct root horizons can be seen at heights of 7.5 and of 16.5 feet above the nodular limestone. These mark periods of fixation in the development of the dune from which the limestone originated. A similar very distinct root horizon also marks the top of the dune limestone (Pl. xv, fig. 3).

Elsewhere the dune limestone is overlain by dune sand which increases in thickness from west to east. Near the south-west corner of the island, the dune sand cover may not be more than 1 or 2 feet, but near the south-east corner, where dune limestone is absent, a recent sand dune rises to a height of 25 feet.

There were once considerable guano deposits on the southern part of the island and it seems that most of them must have been deposited in the depressions between the dune limestone ridges. However, lack of time did not permit a closer investigation of these occurrences. Also, most of the guano has already been removed and the surface relations of the rocks have been much disturbed by human activities.

Along the south coast there are several stretches of short shingle beaches which consist of about half coral shingle, half shells. The coast is bordered by a submarine platform, probably slightly below low-water level, which is between 100 and 200 yards wide. This is an erosion platform, for erosion remnants, indicating a former southward extension of the coast, are still visible in the form of limestone platforms which rise from the submerged flat about half-way between the south-east and south-west corners of the island (Pl. xv, fig. 1).

An interesting feature of the intertidal zone of the cliffs is the abrupt change in the composition of its animal community from the south side to the east and west sides of the island. All along the south side the intertidal zone is characterized by strong growth of *Balanus*, but at the corners these animals disappear rapidly and are replaced by a dense cover of *Ostrea mordax* which extends for several hundred yards along the east and west sides.

There is a strong longshore current along the east coast which carries coral shingle and large shells (*Melo*, *Turbo*, *Trochus*, *Chama*, etc.) to a point about half a mile north of the south-east corner. This current has resulted in considerable silting-up along this part of the coast and in the formation of lagoons which offer some points of interest and may, therefore, be briefly described.

For a distance of about 200 yards north of the south-east corner of the island the coast is formed by the edge of the limestone platform in which the reef limestone rises to about 1 foot above high-water level. About 200 yards from the corner, the edge of the platform turns away from the coast and forms a wide arc inland, only to approach the coast again about half a mile farther north. The bottom of this one-time embayment is formed by reef limestone which has been levelled down approximately to low-water level. A sand bar has been built across this bay, enclosing a lagoon which communicates with the open sea only through a very narrow channel through which water flows at high tide. The sand bar consists of shell sand with a mixed fauna of smaller gastropods and pelecypods such as are characteristic of the tidal zone along the east coast of the island to-day. It is lined along the outer shore by a beach deposit of coral shingle and heavy shells such as are found off the south coast of the island. This material has been swept along the east coast by a long shore current, but its deposition can only have started when the formation of the sand bar was essentially completed, for the latter is remarkably free from coral and heavy shell material. At the present there is probably little addition of shingle material along the beach, but the sand bar is still growing. Its northern end is two-pronged. The eastern prong, pointing outward, is advancing and there is also some silting-up in the bay between the two prongs. The western prong narrows to an acute point and approaches the edge of the limestone platform which here again comes close to the shore. Further north there is a small outlying limestone cliff, 100 yards off the edge of the limestone platform, and this has given rise to the formation of another sand bar which widens towards the north and is separated from the limestone platform by a narrow tidal channel. A small deposit of coral shingle and large shells has accumulated around the outlying limestone cliff.

At high tide, water flows into the depression behind the sand bar where it forms two small salt lakes, whose bottom is formed of a mixture of salt mud and *Coxiella* shells.

#### GEOLOGICAL HISTORY OF EAST WALLABY AND WEST WALLABY ISLANDS.

The site of the two islands was originally occupied by a coral reef composed predominantly of Acroporidae. At some time the growth of this reef was interrupted and several feet of shell limestone were deposited on top of it. The highest parts of this old reef with its overlying shell limestone are to be found in the northern part of East Wallaby Island (Turtle Bay Reef).

After the formation of the shell limestone the reef emerged. At that time the two islands must have formed one continuous platform which extended for some distance beyond the margins of the present island. Calcareous dunes were piled up by south-easterly winds on the southern and northern parts of this platform. There is evidence that, in some places at least, the dunes were formed in a number of stages separated by periods of rest during which they were covered by dense vegetation. Later the dune sands were cemented to form dune limestones.

After this period the island was submerged and limestone boulders were thrown onto the surface of the highest parts of the old reef limestone platform, that must then have stood 16-18 feet lower than at the present day. Then followed a period of emergence during which some coral shingle was deposited also on the lower limestone platforms and around the foot of the dune limestone ridges.

It is not possible to say at what stage the original island was divided into two by marine erosion. It is quite conceivable that this process took place prior to the formation of the dune limestones. Considering the size of the gap now separating East and West Wallaby Islands, it may be assumed that this is a fairly old feature in the topography of the islands. This leads to the interesting conclusion that the low-level platform around and between the Wallaby Islands is probably not a product of Recent erosion and that the fact that at present it is situated at or slightly below low-water level is merely accidental.

#### SUMMARY OF GEOLOGICAL FEATURES OF THE ABROLHOS ISLANDS.

All the larger and probably many smaller islands of Houtman's Abrolhos consist either wholly or at least partly of marine limestones which rise platform-like to a

height of about 6 to 10 feet above high-water level. Locally, however, their elevation may vary between 3 and 16 feet. These limestone platforms consist of a lower coral reef limestone which may rise to any height between high-water level and 4 or 5 feet, exceptionally as much as 11 feet, above high-water level, and which is overlain by 2 to 6 feet of shell limestone which, as a rule, forms the flat tops of the platforms.

It has been shown that East and West Wallaby Islands are largely underlain by limestone of this kind and that smaller limestone platforms also form part of Pelsart Island. Observations from the distance suggest that Middle Island and Square Island of the Pelsart Group consist entirely of such limestone platforms as also do some islands in the northern continuation of Pelsart Island. From available accounts it would seem that Gun Island is of the same nature.

Although I have not visited the Eastern Group, there can be no doubt that, judging from available descriptions, especially that given by Dakin, Rat Island and the small islets to the south of it have the same geological structure, but it is not quite clear if the eastern rim islands of that group (Wooded Island and the islands to the north of it) are made up of the same, or of somewhat younger limestone.

When the Wallaby Group is approached from the south-east, through the passage between the Noon and Morning Reefs, some small limestone cliffs can be seen rising from the submerged reef along the southern margin of Morning Reef; they are obviously erosion remnants of a once more continuous limestone platform. The long island on the north-eastern rim of Noon Reef, however, seems to consist entirely of coral shingle, as has also been observed by Dakin. The limestone platforms of East and West Wallaby and neighbouring islands have already been described in greater detail.

According to Dakin's description, North Island must be very similar to East and West Wallaby Islands, consisting largely of, or underlain by, a limestone platform which rises to a height of 6 to 8 feet above sea-level.

On East Wallaby Island, West Wallaby Island, and from available accounts also on North Island, the high-level limestone platform is overlain by dune limestones, up to 30 feet thick, which are cross-bedded, penetrated by root structures, and consist entirely of calcareous material. In various places on East and West Wallaby Islands the dune limestone forms steeply eroded coastal cliffs indicating a considerable amount of erosion since its formation.

On the high-level platforms are also found unconsolidated shingle beach ridges and on East Wallaby Island there is evidence that these are younger than the dune limestones. From their degree of weathering, however, it may be concluded that they are older than the oldest beach ridges of the low-level platforms.

Islands, or parts of islands, that do not consist of, or are not underlain by, these limestone platforms rise from a somewhat lower platform of coral reef limestone which stands usually somewhere between low- and high-water level. These low-level platforms always seem to consist of reef limestone. Shell limestone has never been found on them except in the form of smaller pocket fillings as described in the section dealing with West Wallaby Island.

On these platforms shingle limestone may have been formed or loose shingle, shell, or sand deposits may have been accumulated, or their accumulation may still be in progress. For example, on the low-level platform of Pelsart Island subaqueous shingle deposits have been formed, cemented into shingle limestone, and later partly eroded. Subsequently, coral shingle beach ridges were accumulated partly on the eroded shingle limestone, partly on the emerging surface of the old low-level platform. Where several systems of such beach ridges are found, as e.g., on Pelsart Island, the innermost ridges, i.e., the ones that are farthest from the shore, are always much more strongly weathered and are in some places up to 5 feet higher than the outer ridges. In places there is a gradual decrease in height from the innermost to the outermost ridges.

Around the edge of the low-level platforms the surface of the reef limestone falls off to varying depths. This surface is irregular and it is still being built up by coral growth in many parts of the islands. Also, from the evidence collected on the Pelsart Group, one may assume that active coral growth is widening the platforms seaward.

Among the youngest deposits on the islands, in many places still in the process of formation, are coquina and shell sand deposits, often in the form of sand spits and bars, certain shingle accumulations, and dune sands; also, a calcareous ooze which is now being formed locally on some of the low-level platforms. Almost everywhere on the islands there is evidence of strong erosion and degradation of the coasts. The limestone cliffs of Pelsart Island, East Wallaby Island and West Wallaby Island are now being cut back, and the same must be true for all other high-level platforms of the Abrolhos. A considerable amount of erosion must have taken place on East and West Wallaby Islands since the formation of the dune limestones. That erosion at present also attacks older beach ridges along the shore has been shown on Pelsart Island.

Thus, at present both constructive and destructive processes are at work modelling the relief of the Abrolhos Islands. Erosion is vigorously attacking most parts of the islands above sea-level. At the same time the islands continue to grow below sea-level and their bulk is continuously being added to by the growth of corals in shallow waters, inside the island groups as well as along their outer margin.

Dakin has already noted that the groups constituting Houtman's Abrolhos from north to south seem to represent stages of development, North Island being the most youthful and the Pelsart Group the most mature of the island groups. This question will receive further consideration in the concluding chapter of this paper.

#### SOME FEATURES OF THE CONTINENTAL SHELF IN THE VICINITY OF THE ABROLHOS ISLANDS.

Houtman's Abrolhos rise from the edge of an almost level submarine shelf which forms the floor of the sea between the islands and the mainland (Figs. 6, 7). Near the mainland coast the sea floor slopes down to about 20 fathoms at a distance of usually not more than 3 miles. The remaining portion of the shelf is practically level, sloping almost imperceptibly to depths between 25 and 28 fathoms on the east side of the Abrolhos Islands, that is, a slope of about 5 to 8 fathoms in a distance of about 25 miles.

The rise of the islands from this shelf is, as a rule, fairly steep, for 20 and 22 fathoms are commonly found quite close to the edge of the coral platforms or islands, as, for example, in Batavia Road on the SE. coast of Pelsart Island, along the outer edge of the eastern rim of the Easter Group, and elsewhere. Also, deep embayments, almost at the average level of the shelf, exist in some of the groups. An example is Good Friday Bay, which penetrates deeply into the Easter Group, with depths up to 18 and 20 fathoms.

Although the position of the edge of the continental shelf is not well known, it seems that the Abrolhos Islands are not situated very close to it. The Admiralty Chart records a sounding of only 42 fathoms, 5 nautical miles west of the edge of the North Island Reef, and one of 85 fathoms,  $11\frac{1}{2}$  miles west of it. West of the Wallaby Group and Middle Channel, the 100-fathom line must be at least 13 miles off the outer reefs. Farther south it swings landward. Off the outer reef of the Pelsart Group, depths of 100 fathoms and more have been found 3 to 4 miles out, and in general the Pelsart Reef does not seem to be more than 5 miles from the edge of the shelf. As has been mentioned above, all the islands are, however, situated at, or very near to, the edge of the 25-30 fathoms platform. On their outer side the sea-bottom slopes down to depths exceeding 30 fathoms.

Some of the island groups are very irregular structures and are composed of a number of separate coral limestone platforms rising independently from the continental shelf. A good example is the Wallaby Group which consists of at least five such independent units. The largest of these is the irregular platform from which East and West Wallaby Islands as well as a number of minor islands rise. To the south and south-west are the Evening, Noon and Morning Reefs. The first-mentioned is atoll-shaped, though entirely submerged, at least at high tide. The Noon Reef encloses an irregularly shaped lagoon and bears a few rim islets; the depth of the sea between these two reefs and between them and the main platform to the north is unknown, but the Noon Reef is separated from the Morning Reef by a narrow channel, not more than a few hundred yards wide, which is 23 fathoms deep, that is, whose bottom is approximately at shelf level. Quite isolated from the rest is the NE. Reef which is separated from the other

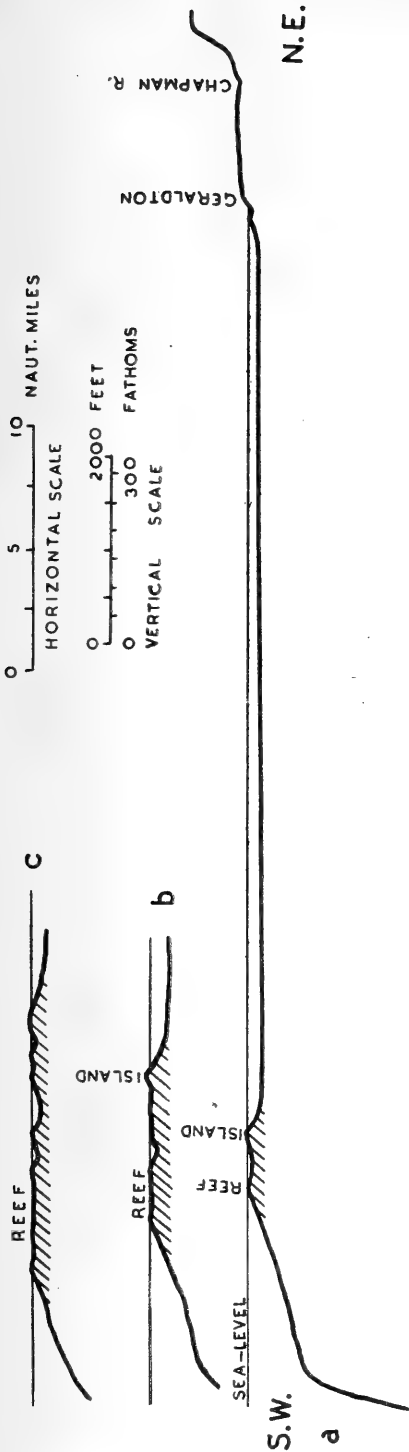


Fig. 6.

Fig. 6.—Profile through the continental shelf between Geraldton and the Pelsart Group and three cross-sections of the Pelsart Group. (For position of sections see Fig. 1.)

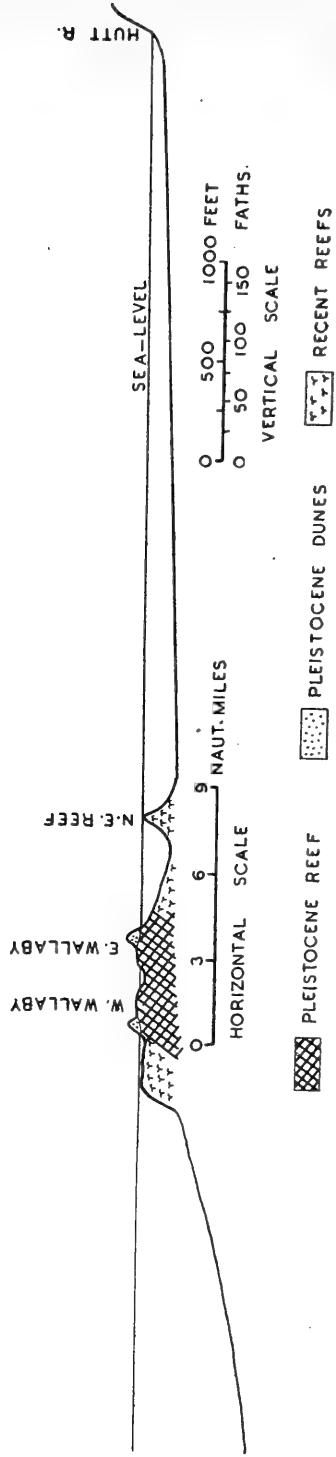


Fig. 7.

Fig. 7.—Cross-section through the continental shelf from the mainland to the Wallaby Group. (Marked "d" on Fig. 1.)

reef platforms by a stretch of water two and a half nautical miles wide and 25 to 27 fathoms deep. This reef, too, rises directly from the continental shelf.

Similarly, the north-east corner of the Easter Group is formed by a platform with some rim islets which is separated from the main platform by a channel which is 25 fathoms deep, and to the north-east of the Pelsart Group we find King Reef and the Hummock Islands, which both rise as separate units from the shelf at depths between 22 and 25 fathoms. Still further to the north-east, about 9 nautical miles from the Pelsart Group, lies Mid Reef, which is only half a mile long and nearly awash, with depths between 22 and 26 fathoms all around. Half-way between the Pelsart and Easter Groups, but several miles to the east, lies Snapper Bank which is 1.7 nautical miles long and 0.8 nautical miles wide and rises from 23 to 26 fathoms of water to within 6 to 8 fathoms of datum. The shelf between it and the Easter Group slopes down to 31 fathoms. King, in 1846, described Snapper Bank as a "coral bank", and it is most likely that it represents a coral reef which is at present growing upward and has not yet reached the surface.

Furthermore, some irregularities of the shelf relief in the north-western and south-eastern continuation of the Abrolhos Group must be mentioned. About 10 miles to the north-west of North Island, on a straight line with the other islands of the group, the Admiralty Chart records a small area of "heavy breakers" which is separated from North Island by water 31 fathoms deep.

In a south-easterly direction, about 23 miles from the south end of the Pelsart Group, under 29° 15' S. Lat. we find Clio Reef, and between 29° 20' and 29° 30' the Turtle Dove Shoal where the sea "breaks heavily at times". The Turtle Dove Shoal rises in water 36 to 49 fathoms deep. Close to it, though separated from it by 37 to 39 fathoms of water, is the Pelsart Bank, 5 nautical miles long, trending approximately NW.-SW., more or less parallel to the margin of the shelf. The Admiralty Chart records here 18 fathoms, but "probably much less water", rising from 35 to 75 fathoms. The occurrence of "coral" is noted both on the Pelsart Bank and the Turtle Dove Shoal and in the vicinity of the Clio Reef, as well as in several places on the shelf between the Clio Reef and the Abrolhos Islands at depths varying from 24 to 50 fathoms.

We may conclude, then, that:

(1). All the groups of the Abrolhos Islands, with the exception of North Island, consist of groups of limestone platforms of irregular size and shape which rise independently from the continental shelf.

(2). These islands and submerged platforms form part of a larger group of elevations on the continental shelf, to which also belong a number of submerged banks and reefs to the north, east and south of the Abrolhos Islands.

#### THE "COASTAL LIMESTONE" OF THE MAINLAND COAST.

Some geological formations of the Abrolhos Islands can be correlated with rocks on the mainland, and valuable evidence in regard to the geological history of the islands may be obtained in this way.

One of the most widespread and most uniform geological formations of Western Australia is a deposit of limestone along a coastal belt which begins in the vicinity of Albany on the south coast and can be followed along the coast of the Indian Ocean into the tropical regions of the State. This formation is usually known as Coastal Limestone. Its lower part very frequently contains marine shells which occur up to varying heights above high-water level. Above this marine limestone lies a series of cross-bedded limestones which rise in ridges and hills and which, as a rule, contain no fossils. A characteristic feature of this part of the Coastal Limestone, however, is the occurrence of root structure of the same type as has been described from the dune limestone of the Abrolhos Islands in an earlier part of this paper.

Considering its wide distribution along the coast of Western Australia, the Coastal Limestone could not fail to impress the early naturalists who visited these shores during the period of discovery, and the interest which these rocks then received contrasts markedly with the scarcity of more recent observations. Since most of the earlier



observers were concerned more or less exclusively with the aeolian part of the limestone, further notes on the views expressed by them will be given later in this chapter.

#### MARINE BEDS.

Some features of the marine portion of the Coastal Limestone were described in a paper by Somerville in 1920. On the shores of Freshwater Bay and Mosman Bay, in the lower Swan River estuary, Somerville found shell limestones rising to a height of 23 feet above high-water level. Such limestones are seen elsewhere on the coast of Western Australia but have as yet received little attention.

An interesting feature in them is the occurrence of emerged coral reefs, and since their study is essential for a better understanding of the geological history of the Abrolhos Islands, at least one of them may here be described in some more detail. The reef with which I am best acquainted is exposed at Point Leander, near Dongarra, 40 miles south of Geraldton. Its existence was first noted by Hartmeyer (1907) who, however, had the erroneous notion that it rested on granite, whereas borings near Dongarra have penetrated sediments to a depth of over 2,000 feet. Campbell mentioned the reef briefly in a report published in 1910 but did not describe it in detail.

The reef forms a small promontory, Point Leander, and extends for about one-third of a mile along the coast. Its upper surface is flat and only a comparatively narrow ledge is exposed below a cover of recent sand dunes. The reef limestone forms a cliff which rises about 12 feet above a platform extending from the foot of the cliff for a distance of about 100 yards to one-quarter of a mile out to sea. This platform is dry at low spring tides. The surface of the reef may, therefore, be between 10 and 11 feet above mean-water level.

The cliff is in places strongly undercut, with overhanging ledges as much as 12 to 15 feet wide, and the structure of the reef can be well studied in these undercut parts. The limestone consists mainly of branching colonies of *Acropora*, but in places spreading, dish-shaped colonies of the same genus are quite prominent. These form layers 1 to 2 inches thick and often several colonies are piled up on top of one another so as to give the reef limestone some kind of bedded appearance. In addition, colonies of *Platygyra* and *Favites*, measuring up to 20 inches in diameter, are liberally distributed throughout the entire reef. Solitary corals are conspicuously absent.

The space between the coral colonies is filled with shell limestone, mostly composed of shell grit with few entire shells, but in places cemented coral débris (broken branches of *Acropora* and fragments and overturned colonies of *Favites* and *Platygyra*) are wedged in between the corals of the reef.

On the whole, this reef is very similar to the reef on the east shore of Turtle Bay, East Wallaby Island, which has been described in an earlier section of this paper. Also, it seems that the coral fauna of the Dongarra Reef, on the whole, is comparable to that of the reef limestones of the Abrolhos Islands, although it might be poorer in species. Thus, *Porites*, *Goniopora* and *Euphyllia* have not been observed at Point Leander, although it is possible that additional species might be found by more systematic collecting.

A very similar raised coral reef is known from Salmon Bay on the south coast of Rottnest Island, but this has not yet been studied in detail.

Reef corals occur in many other places in the Coastal Limestone without, however, forming structures worthy of the name coral reef. Thus large numbers of colonies of *Platygyra* and *Favites* may be seen in the limestone on the coast of North Beach, north of Fremantle. Colonies of the same genera occur also in the Coastal Limestone near Bunbury and I have even observed several of them in depressions in the pre-Cambrian gneisses several feet above sea-level at Canal Rocks, near Yallingup, 10 miles south of Cape Naturaliste, at Lat. 33° 45'.

#### AEOLIAN LIMESTONES.

These marine limestones are, as has already been stated, in many places overlain by cross-bedded limestone deposits which form ridges and hills and seem to represent old calcareous sand dunes which are now cemented. One of the most striking features

of this limestone is the appearance of root-like meshworks of calcareous rods which weather out on the exposed surfaces of the limestone in many places and which could not fail to attract the attention of earlier observers. The structures resemble in all respects those that have been described in an earlier section of this paper from the dune limestones of the Abrolhos Islands.

Regarding the origin of these structures in the Coastal Limestone, three explanations were advanced at comparatively early dates: they were interpreted as corals, as calcareous replacements of roots, and as inorganic concretionary formations. Since these structures have been misinterpreted even in comparatively recent papers, a few further notes on this question may not be out of place here.

Vancouver, on his voyage around the world in 1791, seems to have been the first to notice the occurrence of limestone along the coasts of Western Australia, and in 1798, he gave the first description of its features. He studied the Coastal Limestone in the vicinity of King George's Sound, particularly at Bald Head, and believed the root-like mesh-work which he observed in it to be corals. From this he drew the conclusion that considerable recent elevation of the coast in this place was indicated. Flinders visited the same locality and concurred in Vancouver's conclusions (Flinders, 1814, p. 62). A much more detailed description of the Coastal Limestone was given by the French naturalists Péron and Freycinet (1816, p. 75, pp. 168-73), whose observations in many respects are the most detailed as yet available on this subject. They were the first to realize the wide distribution of the Coastal Limestone along the coast over twenty-five degrees of latitude and, although their conclusions are probably not always free from error, they recognized the resemblance of certain structures in the limestones to the root work of trees. They understood that at least part of the Coastal Limestone is of aeolian origin and they found that shells, leaves, fruits, branches, roots, bones, excrements, trees and trunks all play a part in the formation of these deposits.

The next observer was P. P. King (1827, p. 176), who collected a suite of specimens which was described by Fitton in an appendix to King's *Narrative* (Fitton, 1827, pp. 587-97). Fitton, however (p. 621), regards the "irregular, somewhat tortuous, stem-like bodies" found in some of the limestones as "stalactitical concretions", because they did not seem to exhibit any trace of organic structures.

A brief, but admirable, description of the Coastal Limestone and its root structures was given by Charles Darwin in 1844. During a brief stay at King George's Sound on his voyage around the world, Darwin made an excursion to Bald Head, where the Coastal Limestone is well exposed. Darwin became fully convinced of the subaerial mode of origin of this rock. With regard to the root-like mesh-work in the limestone he says: "These calcareous branching bodies appear to have been formed by fine calcareous matter being washed into the casts or cavities, left by the decay of branches and roots of thickets, buried under drifted sand." But perhaps the clearest and most concise description of these features is found in Darwin's *Journal of Researches, etc.*, published in 1845, where Darwin writes as follows: "The beds have been formed by the wind having heaped up fine sand, composed of minute rounded particles of shells and corals, during which process branches and roots of trees, together with many land-shells, became enclosed. The whole then became consolidated by the percolation of calcareous matter and the cylindrical cavities left by the decaying of the wood, were thus also filled up with a hard pseudo-stalactitical stone. The weather is now wearing away the softer parts, and in consequence the hard casts of the roots and branches of the trees project above the surface and, in a singularly deceptive manner, resemble the stumps of a dead thicket." No better description than this could be given of the most important features of the Coastal Limestone of the Abrolhos Islands to which it applies in every particular.

The subject of the composition and origin of the aeolian portion of the Coastal Limestone received little, if any, attention in subsequent years, but in 1903, Simpson described briefly the main features of the Coastal Limestone of the caves district south of Cape Naturaliste. He regarded the limestone as cemented drift sand, and composed of quartz grains, shell fragments and Foraminifera. He also mentioned the "fossil roots" which abound in the limestone and which are so numerous in places "as to give the rock the appearance of coral". This deceptive appearance has misled even later

observers. In 1934, Fletcher studied the rock, mainly from the point of view of its usability as a building stone, as which it is being widely used. Fletcher's investigation confirmed not only the subaerial nature of much of the Coastal Limestone, but also the origin of the branching bodies in the limestone from roots.

#### AGE.

The wide distribution of the Coastal Limestone, its restriction to a comparatively narrow belt, and its lithological uniformity suggest approximate contemporaneity of all deposits referred to under this name. Also, the usually gradual transition from the lower marine to the upper aeolian section suggests absence of a time break between the two. However, the age of these rocks can only be determined within certain limits.

An upper age limit is set by the occurrence of marsupial remains in caves of the Coastal Limestone in the south-west of Western Australia. These include *Diprotodon*, *Nototherium*, *Sthenurus*, and other extinct forms, as well as remains of the koala bear, the Tasmanian Wolf, the Tasmanian Devil, and others not now found in Western Australia. Browne has recently pointed out (1945) that such faunas, although they are most characteristic of the Pleistocene, may locally well have survived that period, but at any rate they must have become extinct in Western Australia not later than in early Recent time. The latest possible date for the formation of the dune limestones in which these caves occur is, therefore, the late Pleistocene, though they might be slightly older.

As regards the marine section of the Coastal Limestone, Reath (1925) has found that, in the vicinity of Perth and Fremantle, all molluscs belong to recent species, some of which, however, are not known to occur at present south of Geraldton. This indicates deposition of these limestones in water of somewhat warmer temperature than that which is found in the coastal waters to-day. The occurrence of a coral reef in limestones at a similar height above sea-level on Rottnest Island points in the same direction.

It is, therefore, most likely to assume that these marine beds have been deposited during an interglacial stage of the Pleistocene, although it is at present impossible to state with certainty which of the three major interglacial stages is involved.

#### CORRELATION.

Considering the general character of the deposits, there is little doubt that the dune limestone of the Arolhos Islands with its root horizons must be correlated with the upper, aeolian part of the Coastal Limestone of the mainland. The underlying shell limestone and the basal reef limestones would then correspond to the lower, marine beds of the Coastal Limestone. The occurrence of coral reefs in the Coastal Limestone agrees well with this assumption.

#### THE QUESTION OF FORMER LAND CONNECTION.

Helms and Dakin have stated that the Arolhos Islands must once have been connected with the mainland, because certain animals occur on them which, it was claimed, could not have reached the islands across 40 miles of ocean water. The latest available review of the vertebrates of Houtman's Arolhos is that given by Alexander in 1922, from which it appears that two species of indigenous mammals, three species of snakes, nineteen species of Lacertilia, and two species of frogs\* are known to occur there. In addition, the islands harbour twelve species of land birds. Special interest attaches to the two mammals:

(1). The Dusky-footed Rat, *Epimys fuscipes*, which occurs on East Wallaby Island in a variety, probably distinct from the mainland species, which is at present only found along the south coast and on the islands of the Recherche Archipelago.

(2). The Dama Wallaby, *Macropus eugenii houtmanni*, which occurs on the two Wallaby Islands and represents a variety distinct from the typical *M. eugenii* of the mainland where its distribution does not extend much farther north than Perth.

\* Helms (1903, p. 55) listed four species of frogs. See also Parker, *Novit. zool., Lond.*, 42 (1940): 1-106.

It thus appears that at least one, but probably both indigenous mammals of Houtman's Abrolhos are subspecifically distinct from the typical species of the mainland and that the latter are at present restricted to more southern latitudes.

It is well known that vertebrates may make long voyages on floating trees, but the chances for animals to reach the Abrolhos Islands in this fashion are small. There are no big rivers on the mainland opposite the Abrolhos Islands, nor indeed anywhere along the south-west coast, and drift wood, other than flotsam from ships, is almost non-existent on the islands. It seems, therefore, that most vertebrates must have been long established on the islands and must have once reached them on dry foot. Moreover, two further deductions may now be made: The connection between the islands and the mainland must have ceased to exist so long ago that the intervening time has been sufficient for at least one, probably both, species of mammals on the islands to become racially distinct from the original mainland stock. Furthermore, the representatives of the original stock of both mammal species are now restricted to latitudes considerably south of the Abrolhos Islands and are found in regions with an average annual temperature about 5°F. lower than that of the Abrolhos. This seems to indicate that connection between the islands and the mainland existed at a time when the average temperature of that area was so much lower.

Dakin's suggestion that the Abrolhos Islands have been separated from the mainland by river erosion seems to imply the existence of a comparatively thin veneer of coral limestone over a hypothetical foundation of Tertiary rocks, but the extreme flatness of the shelf between the islands and the mainland speaks strongly against river erosion. Also, if, as Dakin suggests, the channels separating the major island groups are the sites of former river courses, one would expect to find some indication of such a river system on the shelf itself. Considering the fact that erosion in the Abrolhos Islands has strongly affected rocks of presumably late Pleistocene age, it would then be necessary to assume that much of this denudation has taken place in post-Pleistocene time, but the features of the shelf do not suggest such youthful erosion. The flatness of the continental shelf between the Abrolhos Islands and the mainland seems to indicate a higher age of this feature which is believed to be older than the islands which it bears.

#### OUTLINES OF THE GEOLOGICAL HISTORY OF HOUTMAN'S ABROLHOS.

Coral reefs on stable continental shelves are somewhat puzzling features which have received comparatively little attention. Davis, in his voluminous treatise on the Coral Reef Problem, devotes only two paragraphs to this category (1928, pp. 358-9), calling attention in particular to the absence of a well-developed barrier reef along the edge of the Sahul shelf. Cadell, in a little-known paper, pointed out long ago (1899) that, in view of the widespread evidence of comparatively recent emergence along the coast of Western Australia, the many coral reefs found off the coast could hardly owe their origin to subsidence, but he had little first-hand information on the coast and none on the coral islands, and was, therefore, not in a position to draw further conclusions from this very sound observation. It is indeed unnecessary, and perhaps impossible, to invoke subsidence in order to explain the origin of Houtman's Abrolhos.

The islands, as has already been described, rise from a flat shelf at depths between 25 and 30 fathoms. Such depths are only little, if at all, beyond the downward range of reef coral growth. Among the most recent authorities Yonge (1940, p. 381) states that "there is little doubt that a depth of some 25 fathoms does represent the maximum vertical range of reef-builders", the controlling factor being light, and Vaughan and Wells (1943, p. 52) say that the maximum depth at which corals are active in building reefs is 46 metres (= 25 fathoms), but that "most reef-building takes place in depths of 15 fathoms or less". It is, therefore, conceivable that the Abrolhos Islands could even have been built up from the shelf under stationary conditions, with the sea-level occupying a position little different from the present, but their history has almost certainly not been quite so simple.

During the Pleistocene the continental shelf between the Abrolhos Islands and the mainland must have been repeatedly above sea-level. Although there are considerable

variations in the estimates of the amount by which sea-level was lowered during periods of maximum glaciation, the most conservative estimates do not put this figure lower than 240 feet or 40 fathoms (Molengraaff and Weber, 1921; Dickerson, 1941), so that even according to such moderate estimates, the area where the Abrolhos Islands are situated would have been dry land several times during the Pleistocene period. Periods of low-water level were periods of cold climate; rising water level indicated improved climatic conditions.

It has been said above that there are indications that the marine portion of the Coastal Limestone was formed during a period when the temperature of the water was slightly warmer than at present. This observation is not incompatible with the assumption of a Pleistocene age of the beds, for it is well known, from observations in Europe, that at various times during the Pleistocene the climate in Central Europe was warmer than now. Similar climatic conditions must also have existed in the Southern Hemisphere, even if the fluctuations of temperature were probably not strictly coincidental in the two hemispheres.

In the beginning of one such interglacial period conditions along the coast of Western Australia must have been generally more favourable to the growth of reef-building corals than they are now, particularly in the marginal areas of the coral reef belt. When the sea rose, as water was gradually being released from its ice-bound state in the Polar regions, the corals could grow up from the gradually submerging coastal platform.

It has already been pointed out that the four major groups of Houtman's Abrolhos seem to represent steps of a physiographic evolution, North Island representing the most youthful and the Pelsart Group the most advanced stage. It seems, therefore, that coral growth started earliest in the south, where now the Pelsart Group is situated, whence it spread northward by stages. The small bank north of North Island may be the youngest member of this chain.

A reef which grows from a limited depth under conditions of a rising sea-level would at first grow as a more or less compact mass until it reached the surface or was uncovered by a lowering of the sea-level. If the sea-level fell, growth might have been inhibited for some time, and the old reef would have died. With rising sea-level coral growth was again stimulated and now took place around the old reef. During periods of stationary sea-level the reef would also tend to expand laterally. At the same time the higher parts of the old reef surfaces would be constantly exposed to erosion, and the general surface of the reef would become rather irregular. This stage has now been reached by the Pelsart and Easter Groups. The slightly larger size of the central island (Rat Island) of the latter group may suggest that this group is slightly younger. In the Wallaby Group marine erosion has only started to dissect the oldest reef surface and in North Island the latter is still largely intact.

It may be that these old reefs grew up during the Mindel-Riss Interglacial. This was probably the longest of all interglacial periods and was at times considerably warmer than the present.\*

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\* Since this chapter was written, early in 1944, F. E. Zeuner's book "The Pleistocene Period" (Ray Society, 1945) has appeared, in which considerable space is given to the question of world-wide correlation of eustatic sea-level changes. I have been greatly impressed by the close agreement between the top level of the highest reef and shell limestones in the Abrolhos Islands with Zeuner's Late Monastirian level, the last, and lowest, of the high sea-levels of the Pleistocene which Zeuner puts late in the last (Riss-Würm) interglacial when the sea rose to only about 20 feet above its present stand. If the early Abrolhos reefs date back to this period, the Pleistocene history of the islands would be shorter and the sequence of events more condensed than is being suggested in these pages. The formation of the dune limestone would fall entirely within the last Interglacial and their erosion would be chiefly post-Pleistocene. The question is whether this condensed time-table leaves sufficient time to account for the considerable amount of erosion to which the older island groups must have been subjected.

Since at this stage it would be quite impossible to offer anything more than suggestions for the Pleistocene history of Houtman's Abrolhos, I have refrained from making any changes in the text as written in 1944. The possible significance of the Late Monastirian level in Western Australia, as well as complications and possible confusion arising out of the fact that this level is almost identical with that of the early Recent period, will be discussed in a forthcoming paper on the geology of Rottnest Island, Western Australia.

At some time near the end of this interglacial period all coral growth in the area must have been extinguished, either by a lowering of sea-level or by a decrease in water temperature, or perhaps by "drowning" of the reefs. After this event a deposit of several feet of shell limestone was formed on top of the dead coral reefs. There was, however, no revival of coral growth.

When the sea-level fell during the ensuing glacial period, possibly the Riss, the reefs formed low flat-topped hummocks, about 150 feet high, at the edge of a wide coastal plain. They were subjected to subaerial erosion and at the same time calcareous dunes, later converted into dune limestones, were piled up on some of their limestone platforms.

For the purpose of the present discussion the Riss and Würm glacial stages may be regarded as one prolonged cold period interrupted by a few short, warmer interludes. During most of Riss-Würm time the shelf and the Abrolhos reefs were dry land. Perhaps only three times did the sea-level rise to its present position or higher. It rose probably highest during the Riss-Würm Interglacial, and according to Browne (1945), a 45-foot terrace which is recognizable along the coasts of Australia may date back to this period. During this time there must have been much erosion of the older reef and shell limestones and for a short time even the highest dune limestone ridges must have been completely submerged. It does not seem as if corals re-established themselves in the area during this time, which was probably essentially an era of marine and subaerial denudation. The steeply eroded cliffs formed by the dune limestones on the east coast of East Wallaby and on the south coast of West Wallaby Island probably originated during this time.

During the latter part of the Würm stage the Abrolhos Islands, now strongly dissected and eroded, emerged again and became once more a series of coastal hills. The climate was somewhat colder and the Dama Wallaby and the Dusky-footed Rat, both now restricted to more southern latitudes on the mainland, settled on these hills.

There must have been additional erosion, but also the formation of more dune sands which are now found, as loose deposits, on West and East Wallaby Islands. Some amphibians and reptiles might also have reached the islands during this time.

The final rise of sea-level, after the glacial period, is a comparatively recent event. From observations in Fennoscandia, we know that at the end of Würm time (*Yoldia* time, Finiglacial), that is, not more than 7,000 or 8,000 years ago, sea-level still stood about 80 metres, or 44 fathoms, lower than now (Sauramo, 1928, 1934).

Then, the climate improved rapidly, the sea-level rose, and the Abrolhos were again isolated from the continent. Corals now were re-introduced into the waters surrounding the islands and soon vigorous reefs must have been growing up everywhere. The reefs now expanded laterally. The reefs fringing North Island and the Wallaby Islands platform on their western sides, as well as the Morning, Noon and Evening Reefs of the Wallaby Group, the outlying reefs of the Easter Group and perhaps also part of the outer Pelsart Reef, are probably largely of this age.

Sea-level rose gradually to about 18 feet above its present position, a figure which agrees so well with similar observations in other parts of the world that it may be concluded that this high level was reached during *Litorina* time, or the younger Neolithic, and Bronze periods of Europe, somewhere between 4,500 and 850 B.C. During this time almost all of Houtman's Abrolhos was submerged, with the exception of the tops of the dune limestone ridges of West Wallaby and East Wallaby Islands, where the Wallaby and the Dusky-footed Rat managed to survive the flood. Large coral boulders, or negroheads, were thrown onto the limestone platform east of Turtle Bay, East Wallaby Island. Perhaps this was a period of violent storms, for no boulders of similar size have been seen on any lower platforms.

At this time the shingle limestone of the low-level platform of Pelsart Island must have been deposited. This is now found in many places on the island, although much has been eroded away during the subsequent period of emergence.

Finally, sea-level fell again. The beginning of this latest emergence of the islands may have coincided with the well-known deterioration of climate near the end of the European Bronze age round about 2,800 years ago. As the islands emerged, coral

shingle was accumulated in beach ridges first on the high-level platforms which were remnants, overlain by shell limestone, of the original surface of the earliest (possible Mindel-Riss interglacial) coral reefs. Later such beach ridges also formed on the gradually emerging low-level platforms which were probably mostly the result of Riss-Würm interglacial erosion. Daly and others have suggested that this negative shift of sea-level took place rather suddenly, but conditions on the Abrolhos Islands, particularly on Pelsart Island, are best explained by assuming that the movement was more gradual and may have been continuous until about 100 or 150 years ago.\*

Assuming that the subsidence of sea-level took place at a more or less uniform rate between the years 850 B.C. and about 1800 A.D., the 8-ft. platforms of Pelsart Island and other islands may have appeared above sea-level round about 500 A.D., which would give an approximate measure of the age of the oldest coral shingle beach ridges on Pelsart Island, and other islands whose limestone platforms do not rise above this general level.

The highest points of the low-level platform of Pelsart Island are now 4 to 5 feet above high-water level and beach ridges may have begun to form on them between 800 and 950 years ago, although the oldest beach ridges were probably not completed and stabilized until 100 or 200 years later. This figure is corroborated by the evidence furnished by the beach ridges themselves, for it was found that in some places on Pelsart Island four distinct systems of beach ridges are recognizable and that the youngest of these which is now being degraded is at least 100 years old. Considering the amount of blackening and corrosion of coral shingle that takes place within the period of 100 years, a figure of 600 years or so for the age of the older beach ridges seems plausible.

Reef growth is still vigorous and new reefs are probably still growing up from the bottom of the shelf, but have not yet reached the surface, forming submerged banks to the north, east and south of the Abrolhos Islands (Snapper Bank, Clio Reef, Pelsart Bank, and other unnamed elevations on the shelf).

At the present time sea-level is either stationary or very slowly rising. Limestone cliffs are being undercut and beach ridges are being degraded, although not on a very extensive scale. Some lines of evidence suggesting the existence of a very slight eustatic rise of sea-level at the present time are also available from other parts of the world (Thorarinson, 1940; Marmner, 1943).

The main events of the geological history of Houtman's Abrolhos may be tabulated as shown in Table I.

The geological history of the Abrolhos Islands is in general agreement with that of the adjacent parts of the mainland coast and is satisfactorily explained by the assumption that the islands grew on a stable shelf under conditions of glacially-controlled oscillations of sea-level. The shelf must have existed before the first coral reefs began to develop, and its origin cannot be discussed here. This is a regional problem. This much may be said, that low-level abrasion during the Pleistocene can have had little to do with its formation, because during interglacial periods sea-level almost certainly fell below the average level of the shelf between the islands and the mainland.

\* This question cannot be fully discussed here. Kuenen (1933) tabulated some evidence from the East Indies, showing that the fall of sea-level might have taken place in two steps, causing two benches at  $1\frac{1}{2}$ -2 metres and at  $\frac{1}{2}$ -1 metre above present mean water level. Steers (1937) described a "lower bench" at high-water level from various islands of the Great Barrier Reef; this he thought indicated a negative movement of sea-level of about 5 feet. The only places where in the Abrolhos Islands anything resembling a lower bench occurs is on the west coast of the southern part of Pelsart Island, where there is a distinct narrow bench at high water level. This may correspond to Steers' lower bench and to Kuenen's  $\frac{1}{2}$ -1 metre bench. As a matter of fact, the top of the reef limestone is found at approximately the same height in many places on Pelsart Island and elsewhere, but from the amount of sediments that have been deposited on top of it, it should be clear that this level is a feature that considerably antedates the Recent emergence. Thus, at least in the Abrolhos Islands, it is possible that older benches now occupy such a position relative to sea-level as to give them the appearance of considerably more youthful features. See also the remarks above concerning the age of the reef limestone platform of the Wallaby Islands.

TABLE I.

	Time.	Geological Processes and Rock Formations.	Movements of Sea-level.	Coral Growth.
RECENT.	Present.	Degradation of outer beach ridges. Undercutting of limestone cliffs.	Stationary or rising.	Period of vigorous coral growth.
	Since about A.D. 1000.	Formation of beach ridges on low-level platforms (Pelsart Island).	Subsiding.	
	About A.D. 500.	Beach ridges on 6-8-ft. platforms (Pelsart and East Wallaby Islands).		
	Prior to 850 B.C.	Negroheads of Turtle Bay Reef. Submarine erosion.	First rising, later stationary.	
PLEISTOCENE.	Latest glacial (about <i>Yoldia</i> time) 6000 B.C.	Subaerial denudation. Migration of mammals to Abrolhos.	Sea-level at least 40 fathoms below present.	No coral growth.
	Riss and Würm glacial periods.	Erosion of dune and reef limestones. Formation of dune limestones.	Sea-level mostly low, with perhaps 2 or 3 periods of high-water level.	
	Mindel-Riss Interglacial.	Formation of shell limestones.	Probably sudden rise of sea-level.	Extinction of coral growth.
		Formation of reef limestones.	Sea-level mostly at present level or slightly higher.	Vigorous coral growth.

As far as Houtman's Abrolhos are concerned the "Antecedent-Platform Theory" of Vaughan, Hoffmeister and Ladd, and others meets all the requirements; there was no subsidence and no low-level abrasion; there was just a conveniently situated platform at a convenient height on which coral could grow during and after the Pleistocene. Oscillations of sea-level at some times stimulated, at other times interfered with, coral growth. If the corals could not grow upwards, the reefs expanded sideways. In the late Pleistocene the corals were entirely driven from the area, only to return as soon as conditions permitted.

#### CLASSIFICATION.

Coral reefs which grew on a perfectly stable foundation with eustatic changes of sea-level as the only controlling factor, are of rare occurrence, for the obvious reason that the coral reef belt coincides very largely with the zone of Tertiary foldings which to this day has remained a zone of crustal instability.

Another peculiarity of the Abrolhos Islands is that here we have coral reefs of the marginal belt which were in existence in the Pleistocene and thus disprove the often-repeated contention that no coral growth was possible in the marginal belt during that period.

The oceanographic conditions of the Indian Ocean are still so poorly known that at present no explanation can be given for the remarkable growth of coral reefs in the Abrolhos Islands during the Pleistocene; nor can we give an answer to the question how it could be that corals re-established themselves at exactly the same place in Recent times, after they had once become extinct.



It is, therefore, not surprising that Houtman's Abrolhos exhibit uncommon features and their classification meets with some difficulties.

As has already been mentioned, Darwin must have been puzzled by the reports of the officers of the *Beagle*, as he did not include the Abrolhos Islands in any of his groups of coral reefs. Helms regarded the islands as fringing reefs and Dakin as atolls, but both conceptions are untenable. The reefs are 40 miles off the shore and thus do not come within the generally accepted definition of a fringing reef, and the presence of old cores of emerged coral limestone in the centre of even the most atoll-like group, the Pelsart Group, is not typical of atolls. Davis (1928, p. 204) suggested that the Abrolhos Islands might be "a former bank atoll", now in the process of "degradational transformation into a new sea-level atoll in the manner described by Agassiz". However, according to definition, bank atolls (Davis, 1928, p. 19) are annular reefs which rise from the outer margin of rimless shoals. This definition does not apply to the Abrolhos Islands.

The Abrolhos Islands are neither barrier, nor fringing reefs, nor atolls. They simply rise from the continental shelf as an isolated reef group, 350 miles south of the Tropic of Capricorn and 150 miles away from any other coral reefs in this part of the Indian Ocean. Very little attention has been given to reefs of this type in English-language publications and we have to turn to the Dutch for further guidance.

The scarcity of coral reefs in the western part of the East Indies contrasts sharply with their abundance in the eastern part, as has been noticed by many observers (Niermeyer, Molengraaff, and others). It is thought to be due to the fact that the Sunda Shelf was dry land during the glacial stages of the Pleistocene period, so that no permanent coral reefs could develop here before the end of the Pleistocene. The principal reefs of the Sunda Shelf are the great Sunda Barrier Reef, the coral reefs of the Bay of Batavia, and the Duizend Islands; in this group may also be included the coral reefs of the Spermonde shelf, off the south-west coast of Celebes. In Molengraaff's classification (1930) all these reefs belong to Group II, which consists of "coral reefs whose development is completely governed by oscillations of sea-level during and after the Pleistocene ice-age".

Darwin realized that the reefs of this part of the East Indian Archipelago were not easily pressed into one of the three classical groups, and he stated that "they lose their fringing character and appear as separate and irregularly scattered patches of considerable area" (Umbgrove, 1928, p. 36). For some reefs of this type Niermeyer, in 1911, introduced the Dutch word "plaatrif" which Molengraaff (1930) translated as "shoal reefs", although it would seem that "shelf reef" would more accurately reflect its meaning. It seems, however, that Niermeyer applied the term in the main to barrier reefs built along the margin of submarine plateaus. He points out that barrier reefs can be observed in the East Indies in all stages. Most of them begin as isolated smaller reefs—single reefs, atolls, etc.—which later become fused to form longer banks and islands. The origin of barrier reefs depends on the existences of platforms (shelves). These platforms are a general phenomenon all over the world and their origin is not connected with that of the reefs—"Geen plat, geen barrière-rif". We thus find here clearly stated by Niermeyer what has later become known as the "Antecedent Platform Theory", which was elaborated by Vaughan in 1919 and other publications.

Umbgrove, in 1928, extended the definition of "plaatrifs" to include the coral reefs of the Bay of Batavia, small reefs which rise from the Sunda shelf in depths between 10 and 30 fathoms. These he called "plaatrifs" or "heuvelvormig rifs". The last term could perhaps best be translated with "hummock reefs".

Hummock reefs then are reefs which grow up as irregular patches of different sizes from a stable shelf, not necessarily near its margin. In less than about 20 fathoms of water, such reefs may grow up even if the sea-level is stationary. Where they are found rising from greater depth, eustatic rise of sea-level will probably have influenced their growth, at least in part.

The Abrolhos Islands fall into this category of reefs. More than that—they are hummock reefs of the Pleistocene, whose history is largely determined by glacially-

controlled oscillations of sea-level. On reading the descriptions of the coral reefs of the Sunda shelf one cannot help being amazed at the youthfulness of these features. Although Umbgrove (1930) does not deny, in the case of the coral reefs of the Spermonde shelf, that some of them may date back to the Pleistocene, there is only indirect evidence for such an assumption. The bulk of these as well as of the reefs of the Sunda shelf, seems to be post-Pleistocene. Considering the fact that all these reefs are situated very near the equator, we might have expected that here, if anywhere, coral reefs could have existed in interglacial periods. But apparently no very definite traces of such reefs have been found.

#### SUMMARY AND CONCLUSIONS.

In the foregoing pages the principal rock formations and loose sedimentary aggregates of Houtman's Abrolhos, the southernmost coral islands in the Indian Ocean, have been described. Particular emphasis has been placed on the description of coral shingle deposits of the intertidal zone and of the beach ridge type, and the difference between the latter and the "shingle ramparts" of certain other coral islands have been discussed. In addition, the morphology of the shelf in the vicinity of the islands is discussed and the Coastal Limestone of the mainland of Western Australia is briefly described.

An investigation of some of the major islands of Houtman's Abrolhos has brought out the following facts which are of importance for the interpretation of the geological history of these coral reefs of the marginal belt:

(1). The core of all major islands is coral reef limestone, rising up to eleven feet above high-water level.

(2). This reef limestone is dissected in various degrees. In many places its surface is levelled down below present low-water level.

(3). Those portions of the reef limestone that are left standing at any height above high-water level are overlain by non-coralline shell limestone, two to five, or even eight, feet thick.

(4). Dune limestones, and in places beach limestones, overlie the shell limestone platforms in many places.

(5). Coral shingle limestone, an intertidal deposit, is found on low-level platforms, where it is now partly eroded.

(6). High-level and low-level platforms bear series of coral shingle beach ridges, and, occasionally, larger coral boulders of the negrohead type. The material constituting the high-level beach ridges is more weathered than that of the low-level beach ridges and is therefore older.

(7). On low-level platforms the coral shingle beach ridges may rest on the planed-down surface of the reef limestone or on irregularly eroded shingle limestone. Where there is a successive series of ridges parallel to the shore, as on Pelsart Island, the height of successive beach ridges often decreases beachward.

(8). There is vigorous growth of live coral in the entire area all around the limestone islands and in many places on submerged parts of reef limestone platforms.

On the basis of this evidence, and from correlation with rocks on the mainland, it is here concluded that the history of the Abrolhos Islands must date back to the Pleistocene, and the suggestion has been made that their first period of growth—formation of the reef limestone—might have been during the Mindel-Riss interglacial period. This assumption will seem acceptable only to those who admit the great length of the Mindel-Riss interval as advocated by Penck and Brückner, Soergel, Zeuner, and others. While it is impossible in this place to discuss questions of Pleistocene chronology, it might be well to bear in mind that alternative views are available and that a greater length of the Riss-Würm interglacial period has been advocated by some authorities. A more exact correlation of older Abrolhos Island rocks can only be attempted on the basis of a broader regional survey in conjunction with a study of contemporaneous deposits on the mainland coast.

Reef growth was inhibited during the later Pleistocene, when the islands repeatedly emerged owing to the fall of sea-level during glacial stages. There was some subaerial

dissection, dune limestones were formed, and the islands were settled by several species of vertebrates whose nearest relatives on the mainland are to-day restricted to more southern latitudes. After the end of the last glaciation, when the sea-level rose again, corals re-entered the area and many new reefs were built.

During the subsidence of sea-level that began in mid-Recent time, systems of coral shingle beach ridges were formed on limestone platforms at various levels. It seems that at present the sea-level is stationary or slightly rising, for limestone cliffs are being undercut and young beach ridges are being degraded.

In conclusion, I wish to emphasize that much systematic work remains to be done, none of which has even been attempted in this paper; modern coral and shelly faunas must be studied and compared with the faunas of the Pleistocene reef and shell limestones, and the faunas constituting the various beach ridges of Recent age must be analysed. Only thus will it be possible to obtain a picture of the environmental changes in the vicinity of the Abrolhos Islands since Pleistocene times. The very existence of coral reefs at this particular place presents a puzzling problem which can only be solved by oceanographic work.

A systematic and detailed study of Houtman's Abrolhos, Pleistocene and Recent coral reefs of the marginal belt, would be rewarded by rich results: they seem to be ideally suited for a general study of the glacially-controlled development of coral reefs under marginal conditions on antecedent platforms during and after the Pleistocene.

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## EXPLANATION OF PLATES VI-XVI.

## Plate vi.

Map of Pelsart Island.

## Plate vii.

Fig. 1.—Aerial view (vertical) of south end of Pelsart Island, from 4,400 feet. (Photo, Department of the Air.)

Fig. 2.—Aerial view (vertical) of central part of Pelsart Island (north end of Mangrove Bay and beach ridge system to the north of the latter). (Photo, Department of the Air.)

## Plate viii.

Fig. 1.—View from Little Island across the reef towards the south-west. The overhanging ledge in the foreground consists of shell limestone. The undercut part is reef limestone. Note coral boulders on the reef, mostly of small size. Incoming tide. (Photo, Government Tourist Office, Perth.)

Fig. 2.—Southernmost point of Pelsart Island (left) and north side of Little Island (right). Note shingle ridge on the limestone platform of Little Island. (Photo, Government Tourist Office, Perth.)

## Plate ix.

(Photos, C. Teichert.)

Fig. 1.—Junction between reef limestone (irregularly weathering below) and shell limestone (stratified above). Little Island, at low tide.

Fig. 2.—South end of Pelsart Island seen from Little Island. Note the limestone "chimneys" in the foreground and the shingle ridge on the limestone platform of Pelsart Island.

Fig. 3.—The same beach ridge as shown in Fig. 2 in the distance, resting on limestone platform.

Fig. 4.—Beach ridge system on outer coast, east of workers' settlement, Pelsart Island. The gradual increase in height of successive beach ridges is clearly seen.

## Plate x.

(Photos, C. Teichert.)

Fig. 1.—Outer edge of Pelsart Reef near its southern bend, at low tide.

Fig. 2.—Inner edge of Pelsart Reef near its southern bend, at low tide.

Fig. 3.—"Negroheads", probably erosion remnants of a higher reef level, on the Pelsart Reef.

Fig. 4.—Intertidal coral shingle deposits with large slabs of *Acropora* in roof-tile arrangement. East coast of Pelsart Island, just north of the southern limestone platform, at low tide.

## Plate xi.

Fig. 1.—West side of Pelsart Island, looking south from the northern jetty. Reef limestone forming low cliff, overlain by bedded shingle limestone and by shingle beach ridges. (Photo, Government Tourist Office, Perth.)

Fig. 2.—Narrow part of Pelsart Island, 1,000 yards north of the northern jetty, looking south. Reef limestone and shingle limestone platform on lagoon side (right) overlain by a system of beach ridges. The edge of the vegetation in the foreground indicates approximate position of H.W.L.S. (Photo, Government Tourist Office, Perth.)

## Plate xii.

(Photos, C. Teichert.)

Fig. 1.—Outer beach ridge on the east coast of Pelsart Island (Batavia Road), now subjected to wave erosion. Note the darkened surface zone of the deposit.

Fig. 2.—Same beach ridge as Fig. 1, to show more detail.

Fig. 3.—High-water level bench in reef limestone, west side of southern Pelsart Island. In the foreground slightly higher cliff of shell limestone.

Fig. 4.—Bedded shingle limestone, overlying reef limestone and overlain by old coral shingle beach ridge.

## Plate xiii.

Fig. 1.—One of the Lesser Noddy Lakes, Pelsart Island. The shore is formed by shingle limestone overlain by old beach ridge. (Photo, Government Tourist Office, Perth.)

Fig. 2.—Surface of limestone platform (shell limestone) with sink hole. East Wallaby Island. (Photo, C. Teichert.)

## Plate xiv.

(Photos, C. Teichert.)

Fig. 1.—Turtle Bay Reef from the south. Top of reef strewn with coral limestone and shell limestone boulders.

Fig. 2.—Surface of Turtle Bay Reef, 16 feet above H.W.L., with boulders.

Fig. 3.—Detailed view of part of Turtle Bay Reef, showing mostly foliose species of *Acropora*.

Fig. 4.—Reef limestone surface, below shell limestone layer, on south coast of West Wallaby Island. The corals are here carved out of the limestone by differential wave erosion.

## Plate xv.

Fig. 1.—South coast of West Wallaby Island. Note the coastal platform with erosion remnants. The coastal terrace is formed by shell limestone. The higher ground is dune limestone. (Photo, Government Tourist Office, Perth.)

Fig. 2.—South coast of West Wallaby Island, showing dune limestone overlying the limestone platform of reef and shell limestone. (Photo, C. Teichert.)

Fig. 3.—Fossil roots in dune limestone. South coast of West Wallaby Island. (Photo, C. Teichert.) Note prismatic compass as scale.

## Plate xvi.

(Photos, C. Teichert.)

Fig. 1.—North-east coast of West Wallaby Island, showing typical shore profile.

Fig. 2.—Collapse of overhanging slabs, due to excessive undercutting and following silting-up of the coast. North-east coast of West Wallaby Island.

A SEARCH FOR THE VECTOR OF *PLASMODIUM PTEROPI* BREINL.

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[Read 31st July, 1946.]

## INTRODUCTION.

Following on the discovery of malaria parasites in man similar parasites were found in the red blood cells of bats and other animals. It was quickly shown that anopheline mosquitoes were the invertebrate hosts of human plasmodia, but no vector has yet been found for the plasmodia of bats, nor have the details of their development in the vertebrate host yet been elucidated.

*Plasmodium pteropi* Breinl (1913) was first described from the flying fox, *Pteropus gouldi* Peters in north Queensland, where it is common in these animals. Human malaria, mostly due to *Plasmodium vivax*, also occurs in parts of this area, *Anopheles punctulatus farauti* Laveran (= *moluccensis* Sw. & Sw. de Graaf) being the vector (Heydon, unpublished data). Surveys of the infection rate in "wild-caught" mosquitoes would be liable to error if anopheline mosquitoes were vectors of *P. pteropi* as well. The immediate object of the present work was to attempt to infect anopheline mosquitoes with *P. pteropi*, and if this was unsuccessful, to extend the work in the hope of finding the vector of this parasite.

## HISTORICAL.

From Italy, Dionisi,\* in 1899, described *Polychromophilus melanipherum* from *Miniopterus schreibersii* and *P. murinus* from *Vespertilio murinus*. He failed to find any segmenting stages of these parasites but as they were pigmented and intracorpuseular they are at present classified in the genus *Plasmodium*. He also described an unpigmented parasite, *Achromaticus vesperuginus*, from *Vesperugo noctula*; this is probably a piroplasm. Three species of mosquitoes, *Anopheles claviger*, *Aedes caspius* (= *Culex penicillaris*) and *Aedes vexans* (= *Culex malariae*) were fed by him on infected bats but none became infected.

The next important contribution is that of Schingareff (1907), who described segmenting stages of *P. murinus* in the peripheral blood, liver and spleen of *Vespertilio daubentoni* but only gametocytes of *P. melanipherum* from *M. schreibersii*. Since his bats always harboured wingless flies of the family Nycteribiidae he dissected six, but found no evidence of infection. These observations were made in Russia.

Vassal (1907), working in Annam, found *Vesperugo abranus* infected with a parasite which he described as *Plasmodium melanipherum* var. *monosoma*. He fed the mosquitoes *Culex pipiens* and *Anopheles subpictus* (= *Myzomyia rossii*) on the bat and dissected them from one to ten days later with negative results.

In 1913, Breinl described *Plasmodium pteropi* from *Pteropus gouldi* in north Queensland, the first record of a plasmodium from a flying fox (Megachiroptera) in Australia. A similar parasite was described by Mackie (1914) in *Pteropus edwardsii* in India; in ignorance of Breinl's prior use of the name, he also called it *Plasmodium pteropi*. In any case the two appear to be identical; the figures show rings, gametocytes and forms which are described as "segmenters". Mackie kept an infected flying fox in a cage with uninfected animals none of which developed the infection, although all were infested with Nycteribiidae. Dissections of some of these flies were without positive result.

Rodhain (1926) described *Plasmodium epomophori* from the epauletted flying foxes of the Belgian Congo; in natural infections gametocytes were always present but

\* Quoted from Manwell, 1946.

schizonts were seldom found and no mature segmenters were ever seen. In captivity the infected foxes were at times attacked by *Cimex lectularius*, none of which developed an infection; neither did *Aedes aegypti* (= *Stegomyia fasciata*) nor species of *Culex* which he dissected several days after a blood feed. There were no permanent ectoparasites such as Nycteribiidae on these foxes. In contrast to this, Rodhain found the common flying fox, *Eidolon helvum*, to be always infested with Nycteribiidae but never to be infected with plasmodia. In fact, it proved refractory to infection by blood inoculation.

#### MATERIALS AND METHODS.

At night, flying foxes range the countryside in search of food, which consists of the blossoms of various trees and fruit, both wild and cultivated, but during the day they congregate in "camps" and rest hanging from the topmost branches of trees. Two such camps were located; one, a mixture of *Pteropus gouldi* Peters and *P. scapulatus* Peters, was in a mangrove swamp on Magnetic Island, near Townsville; and the other, of *Pteropus conspicillatus* Gould only, in a tea-tree swamp on the outskirts of Cairns. In both camps there were young unweaned flying foxes, *P. gouldi* and *P. conspicillatus* respectively (*P. scapulatus* differs in its breeding season from the two former species). If Ratcliffe's (1931) estimation of the month of birth of these species be correct, the ages of the young *P. gouldi* would be one to two months, and of the *P. conspicillatus* two to three months. Those we classed as adults were at least twelve months older.

A very high proportion of the adults of all three species were infected with *Plasmodium pteropi*, nearly all showing gametocytes in the blood. Of the young *P. gouldi*, 9 of 17 were infected, and of the young *P. conspicillatus*, 3 of 23. (See Table 1.) The actual number of positives would be higher than these figures show, as in most cases they are based on a single examination. In the captive animals light infestations sometimes fail to show parasites even in thick films. *Pteropus scapulatus* and *P. conspicillatus* are new host records for *Plasmodium pteropi*.

TABLE 1.  
Frequency of Infections in Flying Foxes.

Species.	Adult.		Young.	
	Positive.	Negative.	Positive.	Negative.
<i>Pteropus gouldi</i>	25	0	9	8
<i>P. scapulatus</i>	10	1	0	0
<i>P. conspicillatus</i>	15	3	3	20

These infections in young animals made it probable that active transmission of the parasite was taking place, so in order to get an idea of what blood-sucking insects were flying about, collections were made in the camps, using man as a bait; some of these insects were later dissected and examined for evidence of infection. If the infection of foxes was taking place in the camp it was thought that a day-biting insect must be responsible. However, we found that the camps were not entirely deserted by night as many of the young were left hanging in the trees and a few adults were always about; this made it necessary to collect at night, too.

Some young infected *Pteropus gouldi* were caught and kept in captivity to be used in attempts to infect mosquitoes. These foxes were shown to be potentially infective by the demonstration of gametocytes in stained films and occasionally by the observation of exflagellation of male gametocytes in blood diluted with saline.

The mosquitoes were usually reared from larvae or pupae collected in the field but in some cases "wild-caught" adults were used. The *Anopheles punctulatus punctulatus* Dönitz were from stock originally sent from New Guinea and which had been reared through many generations in the laboratory. They were from a colony regularly used for the experimental transmission of *Plasmodium vivax* and *P. falciparum* infections.

The flying fox was immobilized by tying it to a board and it was then placed in the mosquito cage for an hour. This method gave fair results with all the species of mosquitoes except *Culex fatigans* Wiedemann. Slightly better results were obtained with this species by allowing the mosquitoes to feed overnight on the infected flying fox



which was confined in a small cage beneath a mosquito net. The fed mosquitoes were collected and kept for periods up to 20 days, some being dissected at intervals. The air temperature was roughly 80°F. and the humidity high. In most cases both salivary glands and midgut were examined.

An attempt was made to feed some "wild-caught" sand-flies of the genus *Culicoides* on an infected animal but this was a failure.

#### RESULTS.

The numbers of the different species of mosquitoes dissected after having fed on infected flying foxes are given in Table 2. Usually both midgut and salivary gland were examined. None showed any evidence of infection.

TABLE 2.  
*Dissections of Mosquitoes fed on Infected Bats.*

Species of Mosquito.	Number Dissected.
<i>Anopheles punctulatus punctulatus</i> .. .. .	125
<i>Anopheles punctulatus farauti</i> .. .. .	3
<i>Anopheles annulipes</i> .. .. .	4
<i>Aedes vigilax</i> .. .. .	54
<i>Aedes aegypti</i> .. .. .	27
<i>Aedes notoscriptus</i> .. .. .	34
<i>Aedes funereus</i> .. .. .	28
<i>Culex annulirostris</i> .. .. .	28
<i>Culex sitiens</i> .. .. .	5
<i>Culex fatigans</i> .. .. .	26

It has been mentioned previously that collections of winged biting insects were made, using man as a bait. Day-biting insects found in the mangrove swamp were *Aedes vigilax* Skuse, *Culex sitiens* Wiedemann, *Culicoides* sp., and *Tabanus* sp. The *Culicoides* sp. has been stated by Lee to be near *C. molestus* Skuse, but perhaps a distinct species. The only night-biter collected was *Culex sitiens*. In the tea-tree swamp, *Aedes vigilax*, *Culex annulirostris* Skuse, and *Aedes funereus* Theobald were present by day; and at night these and *Aedes kochi* Dönitz also. Some of these "wild-caught" insects were examined for evidence of infection (midgut and usually salivary glands as well) but none were positive. The species and their numbers were as follows: *Culicoides* sp., 12; *Aedes kochi*, 8; *Aedes vigilax*, 6; *Culex sitiens*, 18; *Tabanus* sp., 3.

Flying foxes of the three species which we examined (*Pteropus gouldi*, *P. conspicillatus* and *P. scapulatus*) were all parasitized by Nycteribiidae, identified by Lee as *Cyclopodia albertsii* Rond. (= *Cyclopodia pteropus* Rainbow). A number were collected from living and dead flying foxes, which had gametocytes in their blood. In all, forty-nine *Cyclopodia*, about equal numbers of each sex, were dissected, and the midgut, and in almost all cases, the salivary glands as well, were examined for evidence of infection. All examinations were negative.

#### DISCUSSION.

If a mosquito be the vector of this plasmodium it is surprising that no positive result came from the series of experimental feedings shown in Table 2. With the human plasmodia, under laboratory conditions, practically all species of anophelines are susceptible to infection, although in nature most of them take no part in the spread of the disease. It seems most unlikely that anophelines can act as the invertebrate host, especially *A. punctulatus punctulatus*, which is an important vector of human malaria in New Guinea. It seems probable that active transmission of the plasmodium was taking place in the camp in the mangroves at Magnetic Island where many of the sucklings were already infected. Although flying foxes shift camp fairly frequently, this particular one had been occupied for at least a month before our arrival, and as the food supply in the surrounding districts was plentiful, it is not likely that the flying foxes, encumbered with young, had been engaging in migrations. It is probable that the young flying foxes were not only born but also infected in the district. Of the day-biting insects found here it seems possible to exclude *Aedes vigilax* and perhaps also

*Culex sitiens* as vectors, for although we did not dissect many of the latter, it is probable that one of the other *Culex* species would have proved susceptible had this been the vector.

Some other species of mosquitoes such as *Aedes funereus* and *Culex annulirostris*, common in close association with the camps of these animals, also seem to be excluded as vectors.

*Culicoides* is common enough in mangrove swamps but we made no satisfactory test of its susceptibility. It would be worth while considering as a possibility in any future work.

We have consistently failed to find satisfactory evidence of the presence of schizonts in the blood or organs of the bats we have examined. Both Breinl and Mackie figure and describe schizonts but these could have been male gametocytes. Recent observations on this point have come from Manwell (1946) who examined blood and organ smears of flying foxes (*Pteropus gouldi* and *Dobsonia moluccensis*) from New Guinea. From several of the blood smears of *P. gouldi* he describes extracellular segmenters, devoid of pigment, which in some cases resemble the exo-erythrocytic forms of bird malaria. He considers that what has been regarded as a species of *Plasmodium* may be, in reality, more closely allied to *Haemoproteus*, and, as a corollary of this, that it would be more logical to look for vectors among the Nycteribiidae and Streblidae.

Our results with the nycteribiid, *Cyclopodia albertsii*, do not support this suggestion. In addition to the negative results of our dissections there is other indirect evidence against this possibility. We have several times found infected mothers with uninfected sucklings though these mothers had *Cyclopodia* on them. Mackie had a similar experience. Also, as has been mentioned, he kept an infected *Pteropus edwardsii* in a cage with other flying foxes but none of the latter became infected although nycteribiids were present.

#### SUMMARY.

1. In a search for vectors of *Plasmodium pteropi* the mosquitoes listed in Table 2 were fed on infected *Pteropus gouldi*. No positive evidence of infection of midguts or of salivary glands was obtained. These observations seem to show that mosquitoes, especially anophelines, are unlikely to be important vectors of this parasite.
2. Dissections of *Cyclopodia* removed from infected animals were also negative.
3. *Pteropus scapulatus* and *P. conspicillatus* are recorded as new hosts for *Plasmodium pteropi*.

#### ACKNOWLEDGEMENTS.

Permission to undertake this investigation was granted by the Director-General, Commonwealth Department of Health, Canberra, and by the Director, School of Public Health and Tropical Medicine, Sydney. Of the many persons who gave assistance special mention is made of Dr. G. A. M. Heydon, Parasitologist to the School; the Senior Commonwealth Medical Officer, Brisbane; the Medical Officers in Charge of the Health Laboratories at Townsville and Cairns; Lieut.-Col. C. R. Bickerton Blackburn and Major M. J. Mackerras of the Malaria Research Unit at Cairns; Mr. R. Norris of the C.S.I.R. Buffalo Fly Investigation Unit at Malanda and members of their staffs.

Mr. D. J. Lee, Zoology Department, University of Sydney, gave invaluable help in the determination of entomological material.

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CRITICAL NOTES ON THE GENUS *WAHLENBERGIA* SCHRADER; WITH  
DESCRIPTIONS OF NEW SPECIES IN THE AUSTRALIAN REGION.

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(Four Text-figures.)

[Read 31st July, 1946.]

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I. INTRODUCTION.

Although specimens of this genus have been known to science at least since the time of Linnaeus, it was not until 1827 that the present generic name was given, all previously known species having been referred to the genus *Campanula*.

*Wahlenbergia*, as now understood, comprises approximately 120 species, with a distribution confined (except for those in South Asia and a few in Europe) to continents and islands of the Southern Hemisphere. This distribution is, in many ways, very convenient for the systematist, as it permits him to divide the genus into three geographical groups, which are morphologically distinct and have no species in common.

At the present time the greatest number of species is recorded from South Africa; the majority occur between Cape Colony, Rhodesia, Transvaal and the Orange Free State, but a few penetrate still further northwards to Natal and Kenya Colony. Odd species have been described from Abyssinia, while Europe possesses only one or two species, the genus in that region being replaced by the genera *Edraianthus*, *Platycodon* and *Campanula*. In South America another group is found of which the greater part is restricted to Chile, on the slopes of the Andes; a few others appear to the north of this territory.

Members of both these groups show a tendency to become permanent shrubs, a life-form which is rarely encountered amongst species of *Wahlenbergia* in Australasia; on the contrary, the normal life-forms here are either herbaceous perennials or annuals. The third geographical group is by far the most interesting to Australian botanists, but at present our knowledge of the species in this group is very meagre indeed.\*

\* *Index Kewensis* gives 8-10 species for this whole region, whereas up to 90 species are described from South Africa.

† After a preliminary examination of the New Zealand material available, it is probably safe to say that all species from that country—although obviously related—are distinct from the Australian and, for the most part, undescribed. This excludes the "*albo-marginata*" complex.

Their distribution ranges from Australia, New Zealand,† Lord Howe Island and New Caledonia to some of the Pacific Islands, Java, Malaya, India, China and Japan.

*Abbreviations for Names of Herbaria Cited.*

The letters in brackets after localities listed under Distribution denote the herbarium in which the material is housed: (M) National Herbarium, Melbourne. (S) National Herbarium, Sydney. (B) Botanic Gardens, Brisbane. (C) J. B. Cleland. (T) A. J. Tadgell. (A) University of Adelaide. (BM) British Museum (Natural History). (K) Royal Botanic Gardens, Kew. (L) N. Lothian.

II. SYSTEMATIC PROBLEMS.

The confusion which surrounds such species as *Wahlenbergia agrestis*, *W. dehiscens*, *W. gracilis*, *W. marginata*, *W. quadrifida*, *W. Sieberi*, *W. simplicaulis*, *W. vincaeflora* and *W. multicaulis* (and their varieties) is not surprising when one remembers the varying climatic and ecological conditions throughout the vast area mentioned above. Also, lack of comparison with existing types, the wide dispersal of type material and the uncertainty of the actual existence of certain types have accentuated this confusion. Another reason, unfortunately true in the past, but now no longer obtaining, was the attitude of certain authorities who refused to let other botanists consult their important material.

While previous workers have differed considerably on the question of specific delimitations, they agree that these species are extremely polymorphic in all characters which are the normal criteria for identification. Bentham in his monumental "Flora Australiensis" points out that probably *W. gracilis* is allied to the Asiatic species, and mentions that several distinct species have been enumerated by various authors. "But", he says, "they run so variously into one another that they would require to be differently defined in every separate collection." Unfortunately this statement has hindered a better understanding and appreciation of the species involved. Although at first Bentham's contention may appear to be sound, the present author considers it highly misleading, and holds a different view, while still admitting that certain variations may occur within a species. It is maintained that field work, in conjunction with the descriptive text of this paper, will justify the above statement. The classification proposed in this paper is in no way regarded as final, since the collection of subsequent material and data (as well as the availability of type material as yet not examined, e.g., at Prague) may make further changes necessary.

III. HISTORICAL SURVEY.

Up to 1827 all previously collected material of *Wahlenbergia* had been referred to *Campanula*, but in that year Schrader proposed the new generic name *Wahlenbergia* in honour of George Wahlenberg, then Professor of Botany at the University of Uppsala. After drawing up the diagnosis of his new genus, Schrader in "observations" mentions that "*Campanula gracilis* should be moved over to the new genus", yet he did not make the necessary change. Later, when A. de Candolle published his monumental work "Monographie des Campanules" in 1830, we find that the suggested combination has been made. This is an important fact, because the authority for *W. gracilis* is usually cited as Schrader.

Professor Hochreutiner, Director of the Botanical Institute of Geneva (in which herbarium A. de Candolle's types are housed) very kindly furnished me with information which proves this assumption correct. He writes: "*W. gracilis* Schrader is a synonym with *W. gracilis* A.DC., both being founded on *Campanula gracilis* Forster", and "Schrader did not make the new binomial, he [Schrader] says that *C. gracilis* Forst. should be transferred to the genus *Wahlenbergia* . . . the true name for the plant should be *W. gracilis* (Forst.) A.DC."

Unfortunately A. de Candolle's description of *W. gracilis* embraced elements of additional species, and until N. E. Brown's amended description was published, we had only Forster's most inadequate description to work upon.

In 1913, N. E. Brown published in the "Gardener's Chronicle" a revision of species whose range was then supposed to be limited to Australia and New Zealand. This was the first real attempt to give under one head all the then known Australian and New Zealand species, and what was more important, the synonymy relating to them.

N. E. Brown was probably right when he said "the confusion started with the publication of Robert Brown's 'Prodomus' (1810), which placed four very distinct species as varieties of *Campanula gracilis* (Forst.)". But with the continual arrival of collections from New Holland at and about this time, including numerous specimens of *Wahlenbergia*, and also remembering how little understood were the limits of the species, one can only admire Robert Brown for making so few varieties, rather than splitting them into endless species and varieties, without sufficient diagnostic characters to support this division.

It may be of interest to mention that Solander had drawn up and completed not only his MSS. for the plants collected on Cook's first voyage (1768-71), but also a series of figures depicting the greater number of species collected; these being in addition to the well-known Banksian plates. Of such elaborate and careful works, only the Banksian plates have been published, and then more than a century after their compilation. Thus the names which were applied by Solander to *Wahlenbergia* species cannot be regarded as valid. Had this work been published as intended, the correct naming of Australian and New Zealand species would have been a formidable task for Robert Brown, as well as for later botanists. Since he makes no mention in his "Prodomus" of these species, we can only surmise that he did not see these MSS., or if he did, decided against using any of the suggested names.

By the latter half of the last century both Robert Brown's "Prodomus" and A. de Candolle's "Monograph of the Campanulaceae" had become standard works of reference. Many botanists, when listing species of *Wahlenbergia*, copied from these works—another factor which did not help the already confused state of nomenclature. Some authors merely copied the descriptions without acknowledging any authority or publication, and it frequently happened that this later author was erroneously cited as the authority for a species.

About this time Miquel renamed the genus, and in his "Flora of the Dutch Indies" we find *W. gracilis* under the name *Lightfootia gracilis* with A. de Candolle's epithet in synonymy.

#### IV. RELATIONSHIP OF ALLIED SPECIES.

The question as to whether there is any real affinity between the Australian and Asiatic congeners has often been raised. Many botanists when writing about these and other closely related species have commented on the similarity. Although Roemer and Schultes (Pugel, 1793) regarded *Campanula marginata* as synonymous with *C. gracilis*, it was not until 1858 that Hooker and Thompson (*J. Linn. Soc. Lond.*) discussed the exact number of validly described species, and the possible identity of Australian and Indian forms. Although greatly amplified by Hooker in "Flora of British India" (1881), his opinions were not acceptable to many workers. It is regretted that N. E. Brown did not make some mention of this recurring question, and whether he considered the possibility of the species being related is not known.

Whilst not wishing to decry the usefulness of Brown's paper, by this omission, many later botanists, when dealing with this group of species, referred those found near Asia to *W. marginata* A.DC., and those recorded in or near the Australian mainland to *W. gracilis* Schrad.\*

\* This has led Merrill and Perry (*J. Arnold Arb.*, xxii, No. 3, 1941, p. 384) in dealing with *W. gracilis* A.DC. to state: "We believe these collections represent *W. gracilis* A.DC. in the wider sense. They appear to be more like the Australian material passing as *W. gracilis* A.DC. than the Asiatic material labelled *W. marginata* A.DC." Of Brass' numbers given under the above discussion, viz., 11627 and 4640, only the latter has been seen. After a very cursory examination of this material it appears to be a new species (although possibly related to *W. bivalvis* Mer.). I am indebted to Mr. C. T. White, Queensland Government Botanist, for making material from this collection available for examination.

One of the most important papers prior to N. E. Brown's revision is that of Koorder in 1912. This work is a carefully compiled list of all the material he collected whilst in Java a few years previously. Referring to *Wahlenbergia*, Koorder has reduced all the local species to synonyms of *W. marginata* (Thunb.) A.DC., and, while evidence is missing to support the view that a careful examination of type materials had been made, it is obvious by his placing all the discussed species under *W. marginata* (Thunb.) A.DC. that the collections in Java are referable to that species rather than to any other. An examination of the type specimen of *Lightfootia gracilis* Miquel (also collected in Java) supports this view. Unfortunately Brown did not mention this work.

Professor Hochreutiner, writing in "Candollea" about material that he had collected in New South Wales, refers all such collections to *W. marginata* (Thunb.) A.DC., and varieties of that species. This is the most recent systematic paper of a revisionary nature to be completed on the species under discussion.

Apart from the individual papers referred to above, little work of value has been published on this subject up to the present time; the majority of papers are merely check-lists of floras inhabiting certain areas, devoid of all specific descriptions and data, except flowering periods and unreliable lists of synonymy. Without access to the actual material collected, identification is impossible.

#### V. FACTORS DETERMINING TAXONOMIC CHARACTERS.

The precise correlation of morphological features has been neglected in the past, hence an appreciation of the specific identities of many of our plants has been missed. In addition to the staminal filaments (which when better understood should become an important criterion) such characteristics as the growth habit, size and shape of the calyx, corolla and capsule, and the presence or absence of hairs, are all features which must be used when defining species. Despite careful attention to the above characters, specimens have been examined which, in our present state of knowledge, cannot be accurately placed.

Here no doubt environmental conditions (including the particular habitat in which the plants are growing) have a profound effect on the growth habit of the plant. Experimental work has been carried out to determine whether such conditions affect specific characters of any ostensible species. In all cases, while the growth habit, size, shape and texture of the leaves frequently show distinct variability, the floral parts remain essentially unaltered. All variations from the normal exhibit a direct relationship with the conditions encountered, and in no instance was there any doubt as to the identity of the species involved.

The extent of hybridism between species of *Wahlenbergia* probably has been over-estimated in the past, and, although field work has not covered all the species included in this paper, sufficient observations have been made to indicate that very rarely do species of this genus naturally hybridize. The only instance that the writer can find recorded of two species apparently interbreeding concerns *W. bicolor* and *W. consimilis*; the "intermediate" resemblance to the suggested parents, however, is not conclusive, and we may have only another example of variation due to environmental conditions.

As all species under field conditions exhibit the above-mentioned variations in vegetative structure, this has led many botanists to attribute such differences to:

- (a) Hybridism amongst closely growing (but not necessarily related) species.
- (b) Polymorphism (variation) within the species.
- (c) Ecological influences upon the plants.

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[Continued from page 203.]

In my view it is probable that none of the Australian species is related to the "*marginata-gracilis*" complex, which extends over Asia, India, Pacific Islands and Indies, New Caledonia, New Guinea and New Zealand, and may have reached Norfolk and Lord Howe Islands.

Intensive field research and examination of all material in the recognized herbaria of Australia have shown explanations (a) and (b) to be quite overshadowed by the effects of (c), viz., environmental conditions.

Brief mention should be made of reduction and proliferation in the number of perianth segments (both calyx and corolla) which occur frequently in almost all the Australian species described herein. *Wahlenbergia quadrifida* (R.Br.) A.DC., as its specific epithet implies, was described from a "four partite" plant, a form which is fairly common, while *W. gracilentia*, n. sp., will constantly produce 3-7-lobed calyces and corollas on the same plant. *W. consimilis* gives variations of 4 to 6 (rarely 7) lobed corollas, and more rarely the calyx is affected.

The most remarkable instances of proliferation yet encountered are in *W. bicolor*, n. sp. Material collected from Kelior Plains (north-west of Melbourne) furnished specimens with 10 to 15 petals, giving the real "double flowered" plants. Similar specimens have also been recorded from New South Wales. Usually the number of stamens corresponds to the petals, but in such extreme cases as this, abortion of the stamens—and in some cases the styles—takes place. In some species the stigmatic lobes tend to vary, but not to the same extremes as other floral parts. The style itself may vary occasionally, while deviation from normal loculi within the capsule is rare indeed, *W. gloriosa*, n. sp., being a notable example of this.

Colour variations occur throughout these species, and while albinos are rare, hues of pink, mauve, pale and deep blue are commonly seen in *W. Billardieri*, new name. Scent has been detected in isolated cases, but it would not appear to be a constant characteristic.\*

#### VI. PHYLOGENY OF THE GENUS AND SPECIES UNDER DISCUSSION.

Closely related to the Northern Hemisphere genus *Campanula*, *Wahlenbergia* would seem to have branched from the former and migrated southwards. South Africa appears to be the chief centre of distribution, and it is not improbable that the ancestral biotypes spread from there to be strongly influenced by local conditions, thereby producing the diversified group of plants we now find. Sufficient time elapsed to allow an even distribution of later biotypes in their present-day regions of development, viz., South Africa, South America and Indo-Australasia.

Confining our attention to those species found in the last-mentioned area, it is evident that the climatic factor has been largely responsible for evolution of various life- and growth-forms.

Two main life-forms are at once apparent:

(A) Annual, to which group only a few species belong.

(B) Perennial, this group claiming the majority of species described in this paper.

*Annual Species.*—These are found in two distinct geographical areas, but it is of interest that in the majority of cases the flowers are small with a distinct corolla tube. One section of this group is typically ephemeral. Species in this section are very numerous in coastal as well as inland areas of Australia, where the entire life-cycle must be completed with no further moisture than the initial rainfall. Inland areas are normally affected by heavy dews, but they apparently play little part in further development of these plants. Another section is found in India, and species in this section appear to develop as typical mesophytes. There are only three species described as annuals in the following pages, viz., *W. dehiscens*, *W. agrestis* and *W. gracilentia*.

It is unlikely that the numbers of this group will greatly increase, although possibly the last-named species is a complex, embracing several entities. There is only one large-flowered annual form known to the writer, but it is impossible at present to decide upon its exact affinities.

*Perennial Species.*—Unlike the annual species, not only is there a lack of uniformity in the shape and size of the corolla, but almost every growth habit normally encountered

\* See article on such characters by A. J. Tadgell (*Vict. Nat.*, lv, 1938, p. 148).

in herbaceous plants can be found. The smallest-flowered species is possibly a form of *W. quadrifida*, while the largest will probably be found in *W. consimilis*, *W. gloriosa* or *W. vincaeflora*.

Regarding growth habit we find two distinct types:

(i) *Caespitose and Creeping Species*.—These, by means of stolons, frequently form cushions or tufted plants up to one foot across. They reach their major development in New Zealand, where they are limited to one main genotype and several biotypes, i.e., *W. albo-marginata* Hk.f. They are again found at Lord Howe Island, where no doubt a different set of environmental conditions has caused a change in development. The only element of this type found in Australia is *W. saxicola* from Tasmania, and possibly *W. gloriosa* of the Victorian mainland alps. It seems surprising that no examples of this type have yet been located in the high altitudes of Queensland (Mt. Bartle Frère and other neighbouring peaks near Cairns), but further botanical exploration in this region may bring them to light. All species so far described possess large flowers. (The New Zealand species, *W. cartilaginea* Hk.f., lacks a distinct corolla tube.)

(ii) *Upright and Frequently Sub-fruticose Species*.—These show great diversity in the growth habit and they are apparently very sensitive to climatic and ecological conditions, as are the annual-ephemeral forms previously mentioned, thus giving a range of habit which can only be described as protean in character. Plants of the group have proved most difficult to identify; abnormal flowering seasons create further difficulties for the investigator. Here may be cited *W. vincaeflora*, *W. consimilis*, *W. quadrifida*, *W. gloriosa* and *W. bicolor*.

As already emphasized, although the vegetative parts vary considerably, the floral parts remain constant. The elucidation of the conditions causing such different habits in the plants concerned is, therefore, a matter for much further study; only then will their true systematic position be determinable.

Differing principally in habit from those of the last group, there are tall-growing species of *Wahlenbergia* which inhabit areas within the tropics, and a great deal more field work will be necessary before we can finally decide on the true affinities of these plants. They vary greatly in height, possibly due entirely to the environment, and while appearing to belong to the same genotype, may eventually need to be segregated. They possess small flowers, usually with a corolla tube, flaccid leaves with flattened margins, and branching and more or less glabrous stems; the peduncles and pedicels also re-branch to give a many-flowered crown to the plant. I am inclined to believe that several species may be involved in what has been described as *W. marginata* (Thunb.) A.DC.

The evolutionary trend within the genus appears to be limited to the size of the flowers, development of the staminal filaments and of the general pollinating mechanism. At present the maximum development has occurred in temperate regions, and the species which appear to have become most highly developed are *W. consimilis*, *W. vincaeflora* and *W. bicolor*. In general, the larger-flowered types usually inhabit cooler localities, including alpine areas in the tropics (e.g., *W. bivalvis* Merrill; *W. confusa* Merrill & Perry).

## VII. POLLINATION.

Little is known about the pollination process and no conclusive observations seem to have been made.

E. Haviland in these PROCEEDINGS (Vol. ix, 1884, p. 1171) mentions the deciduous nature of the anthers, and the fact that the early loss of these organs has led many to believe in dioecism for the genus. That the anthers mature and shed their pollen prior to the opening of the buds is usually acknowledged by botanists, and Haviland records "the anthers dehisce introrsely in the bud and in contact with the style, which bears several large glands secreting some glutinous fluid, causing the pollen to coat the outside of the style".



During the process of elongation and maturity of the style, the connective ruptures and the anthers are subsequently shed. Pollen adheres to the style from which it may be removed by insects and thus cross-pollination effected or, should this fail, the recurving of the stigmatic lobes will contact the shed pollen and ensure self-pollination.

A. G. Hamilton\* remarks that a small black native bee is the agent. The present writer verifies this, and in addition, has noted at least three different species of native bees, all of which carried pollen of these plants on their bodies when captured. It has also been observed that these bees frequently stay overnight, as well as spending long periods during the day, in the corolla tubes of these plants.

A small amount of nectar is secreted at the base of the corolla tube, under, or at the base of, the filaments, and this has attracted other insects, especially moths, but at the present time it would appear that native bees are the chief pollinating agents.

Lining the inner surface of the corolla tube in larger flowering species are five vertical lines of long silky hairs. Presumably their object is to guide insects to the source of nectar, and thereby assist in pollination of these plants. (Similar lines of hairs are frequently seen on the lower portion of the style; their use as yet is not understood.) These hairs disappear as the stigma matures and it is doubtful if they serve the purpose Hamilton suggests, viz., to catch and retain the pollen so that self-fertilization can be effected should cross-pollination fail.

The above notes refer only to those species which possess a long corolla tube. Species such as *W. quadrifida* appear to be cross-pollinated in the above manner, but lack the line of long hairs in the corolla. It has been observed in these species (*W. quadrifida*) that in freshly-opened flowers, in which the stigmas are not mature, the filaments will deflex under pressure from above and in doing so lower the anthers. From this it can be assumed that insects seeking nectar press down the filaments and in doing so receive a dusting of pollen direct. Upon alighting on another plant, where the stigmatic lobes are mature and, therefore, reflexed, the pollen is removed from the insect as it seeks the nectar. From this it is suggested cross-pollination is effected. Unfortunately sufficient observations have not been carried out to substantiate the validity of these suggestions, which are based on a few isolated observations.

#### VIII. PROPAGATION.

Although normally increased by seed, vegetative propagation by means of stolons, suckers or pieces of detached roots, has been recorded. Often, in ploughed fields, patches of identical material can be located, and these clones are the result of the original plants having been divided. It is of interest to note that it was by the last-named means that horticulturists propagated many of the early introduced species.

#### IX. FIELD WORK.

From the foregoing remarks it can be seen how important it is to collect full diagnostic material. The lower half of the stems of *Wahlenbergia* are usually so distinct that they show very little resemblance, if any, to the upper portions. This is particularly noticeable when we are dealing with some of the "broad-leaved" forms. These bear wide leaves below but the upper ones are often linear (cf., the familiar *Campanula rotundifolia*), and imperfect material gives a completely wrong impression of the entire plant. Because of the fragmentary nature of many specimens collected in the past, many herbarium specimens cannot be identified with any certainty. It is, therefore, strongly recommended that any future field worker should aim at collecting only complete specimens and in this way simplify the labours of specialists who wish to deal with them.

#### X. ACKNOWLEDGEMENTS.

It would be impossible to attempt any critical work of this nature without the whole-hearted co-operation and assistance of many interested people. To Mr. J. Gilmour

\* *Rep. Aust. Assoc. Adv. Sci.*, vi, 1895.

and Mr. A. D. Cotton of Kew Gardens, England, and Dr. J. Ramsbottom, British Museum, all of whom helped me in the matter of securing type material for examination; to Professor B. F. G. Hochreutiner of Geneva, for the excellent set of photographs of A. de Candolle's types, as well as a great amount of valuable information, and also to Dr. C. Alm of Uppsalla, and the Director of Göttingen University for the loan of type material, my deep appreciation of their interest and help is expressed; to Mr. A. J. Tadgell, who not only gave me full use of his field notes and material collected over the last 25 years, but also continually forwarded fresh material and notes; to Professor J. B. Cleland, Adelaide, and the Government Botanists in Australia and New Zealand for making available many dried specimens; and to Mr. J. H. Willis for his most useful and constructive criticisms, my cordial thanks are tendered.

#### XI. KEY TO THE DESCRIBED SPECIES.\*

Stems erect, simple or branching, leaves placed along the stem .....	A
Stems tufted or caespitose, leaves in rosettes .....	AA
A. Flowers under $\frac{1}{2}$ inch in diameter .....	B
Flowers over $\frac{1}{2}$ inch in diameter .....	H
B. Annual .....	G
Perennial .....	C
C. Leaves glabrous or nearly so, margins entire .....	D
Leaves hirsute, margins serrate .....	F
D. Capsule obconic, $\frac{5}{8}$ inch $\times$ $\frac{3}{16}$ inch, leaves linear, $\frac{3}{4}$ inch $\times$ $\frac{1}{10}$ inch .....	<i>W. indica</i>
Capsule obconic, leaves lanceolate, both larger than above .....	E
E. Capsule obconic, $\frac{3}{10}$ inch $\times$ $\frac{1}{8}$ inch, leaves lanceolate-linear-lanceolate, 2 inches $\times$ $\frac{1}{8}$ inch .....	<i>W. simplicicaulis</i>
Capsule elongate-obconic, $\frac{5}{8}$ inch $\times$ $\frac{3}{16}$ inch, leaves lanceolate, $1\frac{1}{4}$ inches $\times$ $\frac{1}{8}$ inch .....	<i>W. quadrifida</i>
F. Leaves linear-lanceolate, denticulate .....	<i>W. agrestis</i>
Leaves lanceolate to broad-lanceolate, serrate .....	<i>W. marginata</i>
G. Floral segments constantly 5, leaves linear-lanceolate .....	<i>W. dehiscens</i>
Floral segments variable, 3 to 7, leaves ovate-lanceolate .....	<i>W. gracilentia</i>
H. Plant tufted, stems very numerous, erect, close-set, leaves linear .....	O
Plant not tufted, open, stems one to few, leaves ovate to lanceolate .....	I
I. Leaves lanceolate, hirsute .....	J
Leaves lanceolate, glabrous or nearly so .....	L
J. Annual, corolla less than $\frac{3}{4}$ inch diameter, tube short .....	<i>W. Capensis</i>
Perennial, corolla more than $\frac{3}{4}$ inch diameter, tube prominent .....	K
K. Calyx and capsule hirsute .....	<i>W. vincaeflora</i>
Calyx and capsule glabrous .....	<i>W. consimilis</i>
L. Leaves usually opposite, rarely alternate .....	M
Leaves usually rosulate, rarely alternate .....	N
M. Corolla more than 1 inch in diameter, calyx half the length of the corolla tube .....	<i>W. gloriosa</i>
Corolla less than 1 inch in diameter, calyx equal to length of the corolla tube .....	<i>W. Billardieri</i>
N. Corolla up to $1\frac{1}{4}$ inches diameter, tube $\frac{2}{3}$ length of corolla .....	<i>W. gymnoclada</i>
Corolla up to $\frac{2}{3}$ inch diameter, tube $\frac{1}{2}$ length of corolla .....	<i>W. Tadgellii</i>
O. Plant glabrous, corolla tube small, $\frac{1}{16}$ inch long .....	<i>W. multicaulis</i>
Plant hirsute below, corolla tube large, $\frac{3}{16}$ inch long .....	<i>W. bicolor</i>
AA. Stems herbaceous, leaves few and scars absent, peduncles simple .....	<i>W. saxicola</i>
Stems woody, leaves many and scars prominent, peduncles branching .....	BB
BB. Leaves totally glabrous, lanceolate and serrate, capsule sub-globose ....	<i>W. limnophalyx</i>
Leaves pilose at the base, lanceolate spatulate, entire, capsule broad-obconic .....	<i>W. insulae-howeii</i>

\* The new species described herein are mainly from Victoria, New South Wales and South Australia; the vast majority of Western Australian and Queensland plants still require names.

## XII. DETAILED DESCRIPTIONS OF SPECIES.

## WAHLENBERGIA INDICA A.DC.

*Monogr. Camp.*, 1830, 146; DC., *Prod.*, vii, 1839, 434; R. Wright,  *Ic. Pl. Ind. orientalis*, 1849, No. 1176; R. F. Hohenacker, *Pl. Ind. orientalis*, 1851, No. 1095.

*Synonymy.*

*Campanula indica* D. Dietrich, *Syn. Pl.*, i, 1839, 753.

*Distribution*: India, where it was first collected by Leschenault. The TYPE is from Nilgiri Hills, south India, No. 284, and is preserved in the Paris Museum. Due to it having been confused with *W. marginata*, its range in that country is at present unknown. It is called by the natives "Aleka".

It may be of interest to note that the material of this species preserved in the National Herbarium, Melbourne, is identical in all details with the type material and may possibly be from the type locality.

*Description*: Probably perennial, with few erect stems, slightly hairy at the base, otherwise glabrous, six to fourteen inches high. *Rootstock* thickened and napiform, often branching. *Stems* one to few, erect or decumbent at the base, six to fourteen inches high, branching usually in the lower third of the plant, rarely simple, slightly hairy and somewhat angular at the base, glabrous and terete above, rarely grooved. *Leaves* usually confined to the lower part of the plant, thin, sessile, alternate, rarely opposite, linear,  $\frac{1}{2}$  to  $\frac{3}{4}$  inch long,  $\frac{1}{16}$  to  $\frac{1}{10}$  inch in width, slightly hairy, usually on the under surface and along the midrib, with few scattered hairs along the lower portions of the margins; margins slightly thickened and recurved, minutely and somewhat remotely serrate, midrib prominent below, obscure and channelled above. *Peduncles* glabrous, frequently long and slender with few linear bracts; *pedicels* 1 to  $2\frac{1}{2}$  inches long, slender. *Calyx* 5-lobed, erect, glabrous, linear-triangular, acute,  $\frac{1}{10}$  to  $\frac{1}{8}$  inch long, half the length of the capsule. *Corolla* campanulate with small tube and spreading lobes,  $\frac{2}{3}$  inch in diameter,  $\frac{2}{3}$  inch long, tube open, half the length of calyx lobes, lobes  $\frac{3}{16}$  inch long, ovate-lanceolate, acute. *Style* simple, half again the length of the corolla tube with three stigmatic lobes at its apex. *Stamens* five, longer than the corolla tube. *Capsule* glabrous, erect,  $\frac{1}{2}$  to  $\frac{3}{4}$  inch in width  $\frac{3}{16}$  to  $\frac{1}{4}$  inch long, obconic, ribbed, valves three, protruding above the rim of the capsule to one-third the length of the calyx tube, three-celled. *Seeds* numerous, ovoid-oblong, minute, brown.

*Discussion*: It differs from *W. marginata* in the larger corolla, sparser and linear leaves, without white margins, while from *W. gracilis* it differs in its almost glabrous habit, linear leaves and almost entire margins.

## WAHLENBERGIA SIMLICICHAULIS de Vries.

*Lehm. Enum. Plant.*, ii, 241.

*Synonymy.*

*W. gracilis* Benth., *Pl. Aust.*, iv, 1864, 497, pro parte.

*Distribution*: At present only known from Western Australia, where the TYPE was collected by Preiss, No. 1887, in "regionibus interioribus Australiae meridionali-occidentibus", Nov., 1840. The TYPE is preserved at the National Herbarium, Melbourne.

Other localities are as follows: Klemattine Island—Davy's Place "Ad flum Avon. York", Preiss, No. 1884, pro parte, (M); Blackwood River, Miss Hester, 1875, (M); Albany, grassy field, Preiss, No. 1890, Sept., 1840, (M).

*Extended Description*: Probably perennial plant, with one to many stems, erect and simple, eight to fifteen inches high, glabrous. *Rootstock* unknown. *Stems* one to many per plant, erect, simple, slender, glabrous, frequently striated. *Leaves* few and widely spaced along three-fourths the length of the stem,  $\frac{1}{2}$  inch to 2 inches long, up to  $\frac{1}{2}$  inch wide, alternate or less frequently opposite (basal leaves frequently sub-rosulate); lanceolate (or rarely oblanceolate) or linear-lanceolate to linear above, acute, very rarely hirsute, and then only with few scattered hairs on the under surface; margins cartilaginous, crenate or undulate, entire or rarely denticulate, midribs prominent above and below. *Peduncles* simple or branched, slender and devoid of cauline bracts. *Flowers* small,  $\frac{1}{2}$  inch in diameter, tube minute, colour not known.

*Calyx* 5 sepals, narrow deltoid, thin texture,  $\frac{1}{10}$  inch long, glabrous, almost twice the length of the corolla tube. *Corolla* 5 petals,  $\frac{1}{3}$  to  $\frac{1}{2}$  inch in diameter, lobes spreading, ovate-lanceolate, tube short,  $\frac{1}{4}$  to  $\frac{1}{3}$  the length of the corolla. *Stamens* 5, filaments ligulate with two incurved lateral wings, edges ciliate. *Style* stout, exerted well beyond the corolla tube,  $\frac{1}{2}$  inch long, with three broad stigmatic lobes at the apex. *Capsule* obconic,  $\frac{1}{2}$  to  $\frac{3}{10}$  inch long, up to  $\frac{1}{2}$  inch in diameter, glabrous, 2 to 3 times the length of the calyx lobes, veined, but frequently not prominently so, valves 3, protruding for half the length of the calyx above the rim of the capsule. *Seeds* minute, dull brown.

*Discussion:* Together with most of the other species described in this paper this species has also been confused with *W. gracilis*. It is totally distinct from that species as from all other members of the *W. marginata* complex. It shows closer affinity to *W. quadrifida* (R.Br.) A.DC. (which, so far, has not been recorded from Western Australia) than to any other species herein described, and may yet prove to be only a form of that species.

Its distribution is not known, but other specimens (incomplete) collected in Western Australia show close resemblance to this species. As with *W. multicaulis* Benth., further investigation is necessary before the specific delimitations can be fully understood.

WAHLENBERGIA QUADRIFIDA (R.Br.) A.DC. Fig. 1.

*Monogr. Camp.*, 1830, 144; Sweet, *Hort. Brit.*, 1839, 3rd Ed., 419; N. E. Brown, *Gard. Chron.*, liv, 1913, 316; K. Domin in *Diels Bibl. Bot.*, vii, 1929, Heft 89, 1192—No. 2986, pro parte.

*Synonymy.*

*Campanula quadrifida* R.Br., *Prod.*, 1810, 561; Poiret, *Encycl. Meth.*, Suppl., xi, 1811, 57; Sprengl., *Syst.*, (Pugillus), i, 1813, 736; Roem. et Schult., *Syst.*, v, 1819, 97; Sweet, *Hort. Brit.*, ii, 1830, 326; D. Dietrich., *Syst.*, i, 1839, 753. *C. gracilis* var. *vincaeflora* R.Br., *Prod.*, 561. *Wahlenbergia gracilis* Benth., *Fl. Aust.*, iv, 1869, 137, pro parte. *W. gracilis* var. *vincaeflora* A.DC., *Monogr. Camp.*, 1830, 142; DC., *Prod.*, vii, 1839, 437; G. Don, *Gen. Syst.*, 1834, 739.

*Distribution:* Due to the confusion which has surrounded this species, its distribution is, as yet, unknown. Its presence in both Victoria and New South Wales can be verified from material collected from these States, but its occurrence in South Australia, despite Black's description under this name, still needs to be verified.

The following specimens of this species are recorded: *Victoria:* Kyenton railway station, 1,687 ft., A. J. Tadgell, Nos. 43 and 46, May, 1939, (L); Yarck, Miss A. M. Bradfield, Sept., 1941, (L); Mont Albert (railway station), N. Lothian, Oct. 1941—May, 1942, (L); Melbourne, King's Domain, N. Lothian, Nov., 1941—May, 1942, (L); Ferny Creek, Dandenong Ranges, 1,600 ft., red loam, under *Eucalyptus obliqua*, J. H. Willis, 11 Jan., 1942, (M); Main Creek, 7 miles south of Arthur's Seat, 250 ft., basaltic soil, J. H. Willis, 18 Jan., 1942, (M); Creswick (railway station), J. H. Willis, February, 1944, (M). *New South Wales:* Jenolan Caves, W. F. Blakely, Nov., 1899, (S); Hornsby (railway station), "seed introduced in gravel from sod-walls", W. F. Blakely, August, 1915, (S); Ashfield, E. Cheel, November, 1917, (S); Berowra, W. F. Blakely, 6 Oct., 1924, (S); Warrembane, no coll., no date, (S).

The TYPE was collected by R. Brown "around Port Jackson" (New South Wales) and is preserved in the British Museum, along with Brown's other types.

*Description:* Perennial, 6 to 15 inches high, one to many slender stems arising from a somewhat fleshy rootstock. *Rootstock* at first simple, later branching and somewhat fleshy, smooth. *Stems* one to many, 6 to 15 inches high, often decumbent at the base, glabrous except for a few scattered hairs at the base, stout below, slender above, terete, smooth or rarely striated, sometimes reddish, branching and then usually from the base. Lateral (leafy) runners often present at the base. *Leaves* usually confined to the lower quarter of the plant, sessile, glabrous except for a few scattered hairs on under surface of midrib and axils; lanceolate or even linear lanceolate,  $\frac{1}{2}$  to  $1\frac{1}{4}$  inches long,

$\frac{1}{8}$  to  $\frac{1}{2}$  inch wide, sometimes reddish, margins slightly thickened, minutely, and often remotely, serrate and undulate (in cauline leaflets or bracts entire), sub-acute or acute, midrib prominent on both upper and lower surfaces, lateral nerves obscure. Leaves on lateral runners ovate spatulate, rarely lanceolate, glabrous and usually entire, more or less flaccid and alternate. Peduncles glabrous, branching in the upper part of the plant to give one-flowered pedicels. *Flowers* blue, rarely white, four to five sepals and petals, corolla spreading. *Calyx* four- or five-lobed, glabrous, erect,  $\frac{1}{8}$  to  $\frac{1}{10}$  inch long,

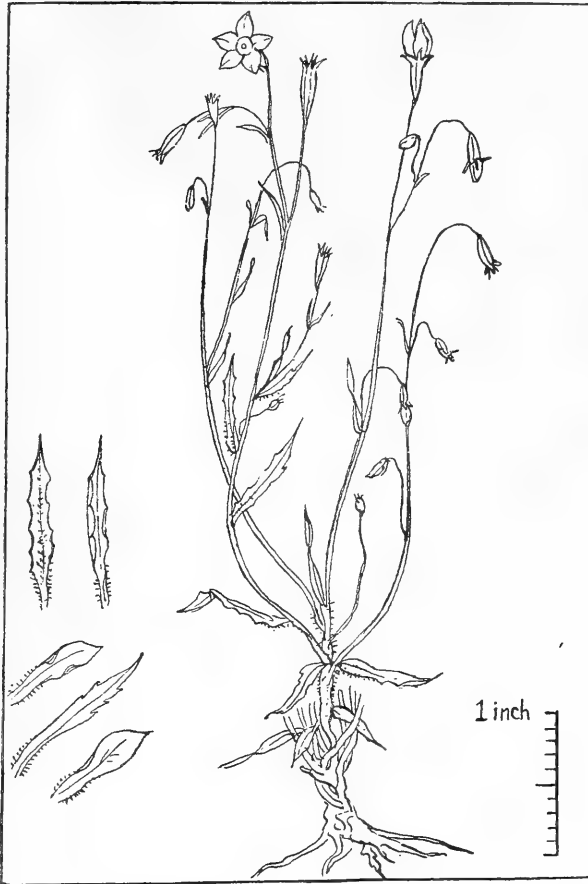


Fig. 1.—*Wahlenbergia quadrifida* (R.Br.) A.DC.

twice the length of the corolla tube or half the length of the corolla lobes (rarely  $\frac{2}{3}$  length), usually appearing between the spreading limbs of corolla. Corolla tube (ovary) obconic,  $\frac{1}{2}$  to  $\frac{3}{16}$  inch long, glabrous, with lines often reddish in colour. *Corolla* blue or pale blue, rarely white, four- to five-lobed; lobes spreading, three to four times length of corolla tube,  $\frac{1}{4}$  to  $\frac{1}{16}$  inch diameter,  $\frac{1}{16}$  to  $\frac{1}{8}$  inch long (deep); lobes when fully expanded ovate-lanceolate, central nerve prominent on under surface. *Stamens* five (or equal in number to corolla lobes), basifixed by slender filament, erect and equal in length to the style. *Style* short but two to three times length of corolla tube, splitting into three broad stigmatic lobes at its apex. *Capsule* glabrous, prominently marked with vertical lines, usually twice the number of calyx lobes and frequently dull red in colour;  $\frac{3}{10}$  to  $\frac{1}{2}$  inch long,  $\frac{1}{10}$  to  $\frac{3}{16}$  inch wide; surmounted by erect calyx lobes which surround a trivalvate apex, three-celled. *Seeds* minute brownish and broad-ovate in shape.

*Habitat*: Appearing to favour open country and readily becoming a wayside weed, but the natural distribution is at present unknown and in need of elucidation.

*Discussion*: A distinct species characterized by its perennial habit, almost radical leaves which are glabrous, spreading corolla lobes and small tube, and elongated capsule. It has frequently been recorded as *W. multicaulis* Benth., from which it is readily separated by the size of the flowers, shape of foliage and broader capsule.

Even after N. E. Brown had described this species in the "Gardener's Chronicle" it was still mistaken for *W. gracilis* (Forst.) A.D.C., possibly owing to his having stated "annual, with one to many stems". Several forms exist, but until their exact relationship with the above can be verified, to mention them here cannot be justified.

It is of great interest that Robert Brown's type material is an example of flowering "runners", i.e., short prostrate lateral shoots, with ascending tips, bearing foliage completely distinct from that normally present. The relationship between these and the normal form is not fully understood, but all evidence strongly supports the view that they are juvenile and adult sets. It may be due to the fact that the type bears this ovate, spatulate foliage that such a complete misunderstanding of this species has resulted.

#### WAHLENBERGIA MARGINATA (Thunb.) A.D.C.

*Monogr. Camp.*, 1830, 142; G. Don, *Gen. Syst.*, 1834, 740; DC., *Prod.*, vii, 1839, 443; Sieb et Zucc., *Fl. Jap. Fam. Nat.*, 1946, 55; Franchet et Savatier, *Enum. Pl. Jap.*, i, 1875, 227; Hochreutiner in *Candollea*, v, 1934, 290 (ex vars.); Tsoong in *Contr. Inst. Bot. Nat. Acad. Piep.*, iii, 1935, 89, pro parte; Kitamura in *Acta Phytotaxonomica et Geobotanica*, x, 1941, 174, pro parte.

This species is treated here in a broad sense and is taken as including a number of forms, some of which have been regarded as distinct species by previous authors. In the present state of our knowledge, however, the writer does not consider that these forms can be referred to any definite taxonomic categories. For convenience, the synonyms and literature cited below are grouped in such a way as to indicate the forms to which they refer in each case. The whole question is discussed further below.

#### *Synonymy.*

*Form A. Agreeing with the type of W. marginata (Thunb.) A.D.C.*

*Campanula marginata* Thunb., *Fl. Jap.*, 1784, 89; *Jap. dec.* 3, tab. 4; Gmel., *Syst.*, 1791, 2, i, 353 (Linn. edit. 13); Willd., *Sp. Pl.*, i, Pt. 2, 1797-8, 905; Poir., *Encycl. Meth.*, ii, 1811, 61; Roem. et Schult., *Syst.*, 1819, 133; D. Dietrich, *Synop. Pl.*, i, 1839, 753, pro parte. This form has also been erroneously referred to *C. gracilis* by Spreng., *Syst.*, (Pugill), i, 1825, 736; to *W. gracilis* by Hook., *Fl. Brit. Ind.*, iii, 1881, 429, pro parte; Forbes et Hemsl. in *J. Linn. Soc. Lond.*, xxvi, 1889, 4, pro parte; Makino in *Somoku Dusetsu-Makino's Edit.*, i, 1907, 176, Pl. 122; Matsum, *Index Pl. Jap.*, ii, 1912, 617, pro parte; Makino et Nem., *Fl. Jap.*, 2nd Ed., 1913, 1174; Matsum, *Index Pl. Jap.*, 1913, 688; Makino, *Illus. Fl. Nipp.*, 1940, 82; Forbes, *Index Fl. Sinensis* (no date), ex vars., pro parte; and to *W. agrestis* by F. Miquel, *Ren. fl. sud., China; J. Bot. Neerl.*, i, 110, pro parte; Benth., *Fl. Hongkongensis*, 1861, 197, pro parte.

*Form B. Agreeing with the type of W. gracilis (Forst.) Schrad.*

*Campanula gracilis* Forst., *Ins. Aust. Prod.*, 1786, 84; Willd., *Sp. Pl.*, i, Pt. 2, 1797-8, 891; R. Br., *Prod.*, 1805, 561, ex vars.; Smith, *Exot. Bot.*, 1805, t. 45; Roem. et Schult., *Syst.*, v, 1819, 97, ex vars.; *W. gracilis* (Forst.) Schrad. in *Blumenbachia*, 1827, 38— in obs.; A.D.C., *Monogr. Camp.*, 1830, 142, ex vars., pro parte; G. Don, *Gen. Syst.*, iii, 1834, 739, ex vars., pro parte; DC., *Prod.* vii, 1839, 437, ex vars., pro parte.

*Form C. Agreeing with the type of W. lavandulaefolia (Reinw.) A.D.C.*

*Campanula lavandulaefolia* Reinwardt in Blume, *Bijdr. Flora von Nederl. Indee*, 1825, 726; D. Dietrich, *Syn. Pl.*, i, 1839, 753. *C. gracilis* var. *hirsuta*, F. Junghuhn in *Natieur en Genweskunged Archief*, 1838, 49. *W. lavandulaefolia* (Reinw.) A.D.C., *Monogr. Camp.*, 1830, 144. *Lightfootia gracilis* var. *lavandulaefolia* (Reinw.) Miquel,

*Fl. Ned. Ind.*, ii, 1857, 567. This form has also been referred to under the names *W. marginata* by Koorders et Schumacher, *Syst. Verzeichen*, i, 1910-13, 136 (Java); *Koorders Excursion Fl. Java*, iii, 1912, 300; *W. gracilis* by F. Junghuhn in *Natieur en Genweskunged Archief*, 1838, 49, ex vars.; F. Junghuhn in *Natieur en Genweskunged Archief*, ii, 1845, 311; and *Lightfootia gracilis* (Forst.) Miquel, *Fl. Ned. Ind.*, ii, 1857, 567.

*Distribution: Wahlenbergia marginata* (Thunb.) A.D.C., sensu lato, extends from Japan—and probably parts of China—to Java and finally New Caledonia. It is possible that collections, other than those compared with certainty with the original collection, will eventually be described as new species, and in consequence the range given above will be more restricted. The types of the various specific names here classed as synonymous with *W. marginata* (Thunb.) A.D.C., their original habitats and the locations of the type material are as follows:

*W. marginata*. TYPE collected by Thunberg at Aroi or Kwana in the province of Mikaw (on the south coast of the island Hondo), Japan; preserved at the Botanical Institute, Uppsala University, Sweden.

*W. gracilis*. TYPE collected by G. Forster in New Caledonia, preserved in the Herbarium of the University of Göttingen, Germany.

*W. lavandulaefolia*. TYPE collected by Reinwardt in the mountains of Java, preserved in Blume's Herbarium in the Museum of Natural History, Paris.

Topotype material of the last two species is represented in the Sydney and Melbourne National Herbaria respectively.

*Description:* Perennial twelve to eighteen inches high, more or less glabrous, with several stems arising from the rootstock. *Rootstock* somewhat woody and branching. *Stems* several, erect, rarely decumbent, simple but more often branching, twelve to eighteen inches high, rarely more than twenty-four inches, somewhat terete, striated, the lower half of the stems and branches bearing scattered white hairs, glabrous above. *Leaves* numerous, sessile, alternate, rarely opposite and then only at the base of the stems and branches, lanceolate to broad-lanceolate, rarely linear or oblong-lanceolate, acute,  $\frac{3}{4}$  inch to 2 inches long, up to  $\frac{1}{2}$  inch in width; lower leaves with short white hairs covering the lower surfaces, the upper surface practically glabrous; margins thickened, frequently greyish-white, undulate, irregularly serrate, sometimes coarsely serrate; upper leaves glabrous on the upper surface, the lower surface with few scattered hairs, usually confined to the midribs, lanceolate to linear-lanceolate, the margins undulate, serrate, slightly thickened and rarely recurved. *Peduncles* rigid, glabrous, slender, naked or with one to few linear bracts; *pedicels* slender, two to four inches long, terete, glabrous. *Flowers* erect, small, blue. *Calyx* erect, five-lobed,  $\frac{1}{10}$  inch long, subulate, acute, glabrous, tube (ovary) ovoid, glabrous. *Corolla* five-lobed,  $\frac{1}{8}$  to  $\frac{1}{16}$  inch long,  $\frac{1}{16}$  inch diameter, infundibuliform, lobes spreading, corolla tube equal to length of calyx lobes. Style slightly longer than the corolla tube with three stigmatic lobes at its apex. *Stamens* five; filaments not seen. *Capsule* erect,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch long,  $\frac{1}{8}$  inch in diameter, ovoid to obconic, rarely broad obconic, glabrous, with six to ten vertical veins; calyx teeth less than half the length of the capsule. Valves three, slightly protruding above the rim of the capsule, three-celled. *Seeds* numerous, minute, ovoid.

*Discussion:* It is of this "species" more than of any other described here that a further very critical examination is necessary of fresh and dried material from all possible localities. It is possible that five or six species may eventually have to be recognized when the forms referred to in the literature cited, and that added at the end of these notes, are more adequately known.

*W. marginata* (typical) is probably the northernmost ecotype of a group of plants extending for some 2,000 to 2,500 miles to the south. Due to the various habitats in which these plants are found, differences occur, but to what extent these differences are of taxonomic significance is at present unknown. *W. lavandulaefolia* (Reinw.) A.D.C. and *W. gracilis* (Forst.) Schrad. are both ecotypes of this same group. Evidence to support this contention is to be found in the habit and size of the inflorescence. It is only the foliage which differs, and this within very narrow limits.

*W. lavandulaefolia*, in its general appearance, is more closely related to the forms previously known as *W. gracilis* than to typical *W. marginata*, but this may possibly be due to the ecological situation from which the specimens were collected, rather than to fundamental morphological or anatomical differences. Typical *W. marginata* is more or less glabrous, the lanceolate leaves having thickened margins which are frequently white. The form represented by *W. gracilis* is more hirsute, erect in habit and taller in growth; the margins of the leaves are thickened but not white. The form represented by *W. lavandulaefolia* lies approximately midway between these two forms. It has the upright mode of growth, together with the branching peduncles of Forster's plant (*W. gracilis*), while the leaves are nearer Thunberg's type specimen of *W. marginata*.

The flowers and inflorescence are almost identical throughout this group, and until further material is available it is considered best to treat all three forms as variants of a single species.

Very few specimens of the typical *W. gracilis* exist. In addition to the type specimen at Göttingen, there are two sheets at the British Museum labelled "W. Anderson, New Caledonia 1774", and also a single sheet in the National Herbarium, Sydney, collected by R. H. Compton, No. 676 (ex Herbarium, British Museum). All these agree with the type and up to the present time I have not seen a similar specimen collected in Australia.

A specimen referred to by Smith (*Exotic Botany*, t. 45), which was raised from seed collected in an unnamed locality in New South Wales, is identical with *C. gracilis* Forst, except in having a hirsute calyx tube (ovary). Until this can be proved a constant feature it has been considered best to include the plant with this species.

WAHLENBERGIA MARGINATA (Thunb.) A.DC. var. NEO-CALEDONICA, new variety.

Affinis *W. marginatae* sed hirsuta, a basi imprimis, et infra et supra superficie foliorum inferiorum rigidis pilis sparse, marginibus paulum cartilagineis, raro albis, inique et crasse serratis; superioribus foliis supra glabrosis, infra paulum hirsutis; floribus et capsula simili *W. marginatae*.

It differs from *W. marginata* in the following details: Plant hirsute for at least three-fourths the height of the stems and branches, densely so at the base. Both surfaces of the lower leaves covered with stiff, short hairs; upper leaves glabrous above and slightly hirsute below; margins slightly thickened, rarely greyish-white, irregularly and coarsely serrate. This variety was included with other forms under the name *Wahlenbergia gracilis* by N. E. Brown (*Gardener's Chronicle*, liv, 1913, 316, and by Cheeseman (*New Zealand Flora*, 1930, 890).

*Distribution*: At present only known from New Caledonia. The TYPE is preserved in the herbarium at the Royal Botanic Gardens, Kew (England) and bears the label "Presented by the Corporation of Liverpool 1885". A further collection by J. F. Roberts, labelled "Mountains 1886" is also referable to this variety.

*Discussion*: From Cook's various expeditions two distinct forms of this species of *Wahlenbergia* were forthcoming, both collected in New Caledonia. One of these two, the type specimen of *Campanula gracilis* Forst., is more closely related to typical *C. marginata* Thunb.; the other is described above as a variety. It may have been collected either by Forster or by W. Anderson, whose name appears on a sheet of material (in the British Museum) which is identical with the type at Kew.

N. E. Brown described this variety under the name of *W. gracilis* (Forst.) Schrader, under the impression that it was the type specimen of *C. gracilis* Forst. However, the actual type specimen is now known to be at Göttingen, so his evaluation cannot be accepted.

The above variety may be only a xerophytic form of *W. marginata*, but until fresh material is collected, it appears best to separate it as a variety. Judging from the material available for study, this form appears to be the more prevalent, but further collections would not only clear up this point but also show its proper relationship



with (a) *Campanula gracilis* Forst., (b) *C. marginata* Thunb., and (c) *C. lavandulaefolia* Reinw.

There is, in addition to the above, a puzzling sheet of material in the National Herbarium, Melbourne. It bears one of R. Schlechter's labels, which states: "*Wahlenbergia gracilis* A.DC. no 14739, 'Bei den Huegeln, Yaouhe, New Caledonia'." Possessing a definite rosette of broad spatulate leaves  $1\frac{1}{2}$  to 2 inches long and up to  $\frac{3}{4}$  inch in width, naked peduncles 6 to 8 inches high then branching in a pseudo-dichotomous manner, flowers larger than *W. marginata* or its variety *neo-caledonica*, it bears a closer resemblance to some of the South African species (e.g., *W. arenaria* A.DC.) than to any Australasian species at present known to me. As many of Schlechter's specimens bear South African labels, it is possible that this, and similar sets of material, have inadvertently become mixed with collections made in South Africa. Until these specimens can be shown to be definitely extra South African in origin, their connection with New Caledonia is a matter for doubt.

#### *Indeterminata.*

Specimens noted in the following references, because of insufficient information contained therein, cannot be identified specifically, and until the material referred to can be examined, their identification must remain uncertain. The references are listed below under the names used by the respective authors.

#### *W. marginata.*

Mori, *Enum. of Pl. Corea*, 1921, 340; Sasaki, *Pl. Formosa*, 1928, 393; Nannf. in *Act. Hort. Gothob.*, v, 1930, 31; Handel, *Mazzetti Symbalae sinicae*, vii, 4, 1081.

#### *W. gracilis.*

Benth. in *Enum. Pl. quas in Novae Holl. Hugel*, 1837, 75; Kurz in *J. As. Soc.*, ii, 1877, 209; F. Bailey, *Qd. Fl.*, iii, 1900, 922; Diels, *Fl. Cent. China*, 1901, 606; Prain, *Bengal Pl.*, 1903, 635, No. 509; Kwakani, *T. Pl. Formosa*, 1910, 900; Léveille, *Pl. du Yun-an*, 1915-7, 26; Lui, *Cowdy coll. of Chihli Fl.* (Chefoo), 1925, 161; Ganguy in *Lecomte Fl. Gener. Indo-Chine*, iii, 1930, 688; Terasaki, *Jap. Bot. Illus. Album*, 1933, t. 1190; Honda, *Nomina Pl. Jap.*, 1939, 337; Nicholson, *Gard. Dict.*, iv, 1890, 190; Matsum in *Tokio Bot. Mag.*, xiv, 1900, 58; A. Usteri, *Kenntoria der Philip. Veg.*, 1905, 120; Matsum et Hayet, *Enum. Pl. Formosa*, 1906, 215; Hayet, *Fl. mont formos.*, 1908, 145; Dunn et Tulch, *Fl. Kwong et Hongk.*, 1912, 52; Franchet et David (no date), 192; Masamune, *Prelim. Rep. Veg. of Yakusuma*, 1929, 124; Masamune, *Fl. et Geobot. Isl. of Yakusuma*, 1934, 434; Brown, *Plants of India* (Lawson's Herbarium).

#### *Campanula gracilis.*

*Hortus Kewensis*, 2nd Ed., 1810, 344; Spreng., *Syst.*, i, 1825, 736; D. Dietrich, *Synop. Pl.*, i, 1839, 753.

#### WAHLENBERGIA AGRESTIS (Wallich) A.DC.

*Monogr. Camp.*, 1830, 145; G. Don, *Gen. Syst.*, iii, 1834, 740; R. Wright, *Icon. Pl. Ind. orientalis*, 1849, 1175; J. D. Hooker et Thompson, *Proc. Linn. Soc. Lond.*, ii, 1858, 21; Drury, *H'book Ind.*, ii, 1866, 104; Hook. f., *Fl. Brit. Ind.*, iii, 1881, 429, pro parte; Daly et Gibs, *Bombay Fl.*, no date, 134.

#### *Synonymy.*

*Campanula agrestis* Wallich in Roxb., *Fl. Ind.*, ii, 1824, 97; D. Dietrich, *Syn. Pl.*, i, 1839, 753.

*Distribution*: India; Bengal, Khasia Mountains; Ceylon; probably also in the lower part of southern India. The TYPE was collected by Wallich in Nepal in 1821 and is now preserved in the Herbarium of the Conservatory of the Botanic Gardens, University of Geneva, Switzerland. Further specimens have been collected in the Palmyry Mts., Sept., 1830, ex Herb. Wright, No. 1280. Much of the subsequent material collected has been hopelessly confused with *W. dehiscens*, *W. indica* and *W. marginata*, so that its full range in India—and its occurrence elsewhere—will remain unknown until this material has been correctly determined and fresh material gathered.

*Description*: Almost glabrous perennial (?), 6 to 15 inches high, stems erect, slender, glabrous. *Root* slender, fibrous. *Stems* 6 to 15 inches high, branching from the apex of the root into several slender, erect, terete, and slightly striated stems, with few scattered hairs below, glabrous above. *Leaves* numerous and confined to the lower third of the plant, 1 to 2 inches long,  $\frac{1}{4}$  inch wide, alternate or sub-opposite, linear to linear-lanceolate, acute; lower leaves with few scattered hairs on the lower surface, margins minutely serrate, undulate, rarely thickened or whitish, frequently somewhat recurved; upper leaves glabrous with entire margins. *Peduncles* slender and glabrous, pseudo-dichotomous branching; *pedicels* filiform. *Calyx* five-lobed, erect, glabrous, subulate,  $\frac{1}{12}$  to  $\frac{1}{10}$  inch long, tube (ovary) ovoid. *Corolla* five-lobed, pale blue, infundibuliform,  $\frac{1}{8}$  to  $\frac{1}{6}$  inch long, rarely more than  $\frac{1}{8}$  inch diameter, twice the length of the calyx lobes, lobes lanceolate, somewhat spreading. *Stamens* five, base of filaments broad, ciliated. *Style* equal to the length of the corolla tube, with three minute linear stigmatic lobes at the apex. *Capsule* glabrous, ovoid-obconic,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch long,  $\frac{1}{8}$  inch wide, valves three, rarely rising above the rim of the capsule, three-celled. *Seeds* numerous, minute, shiny.

*Habitat*: Most literature cites "in and about rice fields", but whether it is common in other habitats is not known.

*Discussion*: Its nearest ally is probably *W. marginata* (Thunb.) A.DC., from which it differs in its more slender habit, linear and almost entire leaves, slightly smaller corolla and capsule valves sunken below the rim of the capsule.

So far as I can ascertain, there are no specimens of this species in any Australian herbaria. Because of this the foregoing description has been drawn up from the original type description.

It is possible that with further material this species may prove to be only a form of *W. marginata* (Thunb.) A.DC.

#### WAHLENBERGIA DEHISCENS (Roxb.) A.DC.

*Monogr. Camp.*, 1830, 145, No. 20; R. Wright, *Icon. Pl. Ind. orientalis*, 1849, No. 1175, pro parte.

#### *Synonymy.*

*Campanula dehiscens* Roxb., *Cat. hort. beng.*, 1814, 89; Roxb., *Fl. Ind.*, ii, 1824, 96; D. Dietrich, *Syn. Pl.*, i, 1839, 735; Roem. et Schult., *Syst.*, 1819, 157, No. 228; Wallich, *Asait. reser.*, xii, 580 (571?), t. 6. *W. marginata* Nannf. in *Act. Hort. Gothob.*, xxxi, 1930, part. *W. gracilis* Kurz in *J. As. Soc.*, ii, 1877, 209, part; Hook., *Fl. Brit. Ind.*, iii, 1881, 424, part; Prain, *Bengal Pl.*, i, 1903, 635, No. 509?; Bourne, *Pl. Ind.* (based on Lawson's Herbarium?). *Roella pauciflora* T. S. Ralph, *Enum. Pl.*, No. 148.

*Distribution*: This species appears to be limited to India, where it has been collected by Roxburgh in Bengal, A. C. Challerjee in Vezpore (Assam) and T. S. Ralph in Mahabules Hwar. The type was collected by Wallich (No. 1294) and is preserved in de Candolle's Herbarium at the Conservatory of the Botanic Gardens, University of Geneva, Switzerland.

*Description*: An annual, 6 to 15 inches high, stem erect, simple, slightly hairy at the base, otherwise glabrous. *Rootstock* slender napiform, rarely branching. *Stem* one, usually simple, erect, rarely branching from the lower part, 6 to 15 inches high, slightly hairy at the base, glabrous above, ribbed and slightly angular. *Leaves* sessile, alternate or opposite, usually limited to lower third of the plant, lower ones with few scattered spreading hairs on lower surfaces and/or along the margins near the axils, rarely entirely glabrous; linear-lanceolate to lanceolate (basal sometimes obovate-lanceolate),  $\frac{1}{2}$  inch to  $1\frac{1}{2}$  inches long, up to  $\frac{1}{4}$  inch in width; margins slightly thickened, undulate, remotely and minutely serrate; upper leaves somewhat smaller and entirely glabrous. *Peduncles* glabrous, rigid, branching from the main stem on upper half of the plant, 2 to 4 inches long, naked except for a few linear bracts; *pedicels* slender, 1 inch to  $1\frac{1}{2}$  inches long. *Calyx* five-lobed, glabrous, linear-subulate, corniform at the apex,  $\frac{1}{16}$  to  $\frac{1}{12}$  inch long, tube (ovary) sub-globose, glabrous. *Corolla* five-lobed, blue to white, infundibuliform,  $\frac{1}{10}$  to  $\frac{1}{8}$  inch long, rarely more than  $\frac{1}{8}$  inch in diameter, lobes ovate-

lanceolate, acute, spreading, tube equal to the length of the calyx lobe. *Style* simple, somewhat robust, half again the length of the corolla tube with three stigmatic lobes at its apex. *Stamens* five, equal to the length of corolla tube, filaments hairy. *Capsule* erect,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch in diameter, broad-ovoid to ovoid-obconic, glabrous, three-valved, protruding to half the length of the recurved and somewhat hooked calyx teeth; three-celled. *Seeds* minute, numerous, oblong-ovoid.

*Discussion:* A distinct species characterized by its almost glabrous habit, lanceolate leaves, undulate and serrate margins, broad-ovoid to almost sub-globose capsule and corniform calyx teeth. It has usually been included with *W. marginata*, from which it differs in the unthickened margins of the leaves, the size of the capsule and the calyx lobes.

WAHLENBERGIA GRACILENTA, n. sp. Fig. 2.

Planta annua, 5–25 cm. alta, brevibus et albis pilis sparsa; caule erecta simplici, per longitudinem paucis ramis; foliis paucis, sessilibus, alternis (saepe infra oppositis)—ovato-lanceolatis, lanceolatis vel oblongis, acutis, hirsutis, 1–2.5 cm. longis, 0.25–1.2 cm. latis, serratis; pedunculis gracilibus, glabris; pedicellis multis; floribus parvis, corolla caerulea, 3–6 fida; calyce 3–6 lobis, glabra, acuta vel subacuta; ovario ovoideo, glabro, seminibus multis.

*Synonymy.*

*Wahlenbergia gracilis* A.D.C., *Monogr. Camp.*, 1830, 144, pro parte; DC., *Prod.*, vii, 2, 1839, 433, No. 47, pro parte; J. D. Hooker, *Fl. Tasm.*, 1860, 239, pro parte; G. Bentham, *Fl. Aust.*, iv, 1869, 139, pro parte; J. M. Black, *Fl. S. Aust.*, iv, 1929, 546, pro parte, Fig. 239B; Flora of King Island, *Vict. Nat.*, iv (9), 1888, 143. *W. gracilis* var. *littoralis* Hook f., *Fl. Tasm.*, 1860, 239, pro parte. *W. gracilis* var. *minutiflora* F. Bailey, *Fl. Qd.*, iii, 1900, 922, pro parte (nom in disp.). *W. quadrifida* J. M. Black, *Proc. Roy. Soc. S. Aust.*, lviii, 1934, 183.

*Distribution:* The following list gives all the known localities, but is by no means complete, serving only to indicate the type of country it inhabits. Although not as yet recorded for northern Australia, nor extensively for Queensland, it should be looked for in these States, in habitats similar to those described below: *Victoria:* Flinders Island, Dr. J. Mulligan, No. 629, 21 Nov., 1845, TYPE, (M); Grampians Mt. William, no coll., No. 29, 21 Nov., 1873, (M); Darebin Creek, F. v. Muell., no date, (*W. gracilis* var. *pentamera*), (M); Darebin Creek, F. v. Muell., Jan., 1852, (*W. gracilis* var. *quintamera*), (M); Dimboola, F. M. Reader, 13 Nov., 1891, (M); Wycheproof district, W. Watts, No. 1407a, Oct., 1918, (M); Bendigo, Whipstick Scrub, A. J. Tadgell, Nos. 48–9, Sept., 1938, (L); Dec., 1939, (L); Sandringham-sands area, N. Lothian, Sept., 1941, typical, (L); Reedy Creek, F. v. Muell., Aug., 1854, "*W. gracillima*", (M); Wimmera, Chas. Walter, no date, (M); Swan Hill, Dr. Gummon, no date, (M); no locality, no coll., no date, "*gracilis* var. *minor*" (F. v. Muell. ?), (M); near Ni Ni Well School, J. Galbraith, Oct., 1941, (L); Glenlee, J. Galbraith, Oct., 1941, (L); Brisbane Ranges, J. H. Willis, 30 Oct., 1943, (M). *Tasmania:* South Esk R., Gunn, No. 740, (M); Bellerive, L. Rodway, Feb., 1893, (S); no locality, no date, J. D. Hooker, (S); no locality, no date, Stuart, "*W. gracillima*", (S); King Island, no coll., no date, (M). *South Australia:* St. Vincent's Gulf, F. v. Muell., 16 Sept., 1848, (M); Bugle Range, F. v. Muell., 23 Sept., 1848, (M); Port Lincoln, I. S. Browne, 1874, (M); Hold Fast Bay, F. v. Muell., 31 Jan., 1878, "*W. gracilis* var. *capillaris*", (M); Mt. Lyndhurst, Max Koch, No. 337, Oct., 1898, (S); Mooloolo Station, between Beltona and Blinman, 8746/15, Mrs. R. S. Rogers, Oct., 1915, (C); Beltona, J. B. Cleland, 5 Dec., 1934, (C); Kinchina, J. M. Black, Oct., 1926, (C); South of Hallett's Cove, J. B. Cleland, 20 Oct., 1932, typical form, (C); Bach Valley, Encounter Bay, J. B. Cleland, 28 Oct., 1934, (C); Bach Valley, off Inmen Valley, J. B. Cleland, 25 Oct., 1934, (C); between Pts. Germein and Augusta, J. B. Cleland, 3 Nov., 1936, (C); Middlebach Station, Encounter Bay, J. B. Cleland, 5 Nov., 1936, (C); Deep Creek, Tate Soc. Exped., J. B. Cleland, 11 Dec., 1938, (C); National Park, J. B. Cleland, 19 Oct., 1935, 7 Oct., 1939, 30 Oct., 1939, 12 Oct., 1941, (C); Kangaroo Island: Rody River, J. B. Cleland, 3 Feb., 1934, (C); Ravine de Carvair, J. B. Cleland, 5 Dec., 1934, (C); no locality, no coll., no date, "*W. gracilis* var.

*pinnatifida*", (M). *Western Australia*: "S.W. Australia", Preiss, Nos. 1883 and 1886, (var. "*quadrifida*"), (M); King George's Sound, J. R. Muir, no date, (M); Lake Giles, Burkett, no date, ("*W. pusilla*"), (M). *New South Wales*: Yanco Experiment Farm, E. Breakwell, Nov., 1913; Temora, Rev. J. W. Dwyer, Nos. 829/15; 6997/15, Sept., 1915, (S); also No. 1095/16, (S); Lake Cargelligo, Rev. J. W. Dwyer, Nov., 1915, (S); *Queensland*: Brisbane, dry hills, no coll., no date, No. 108, (M).

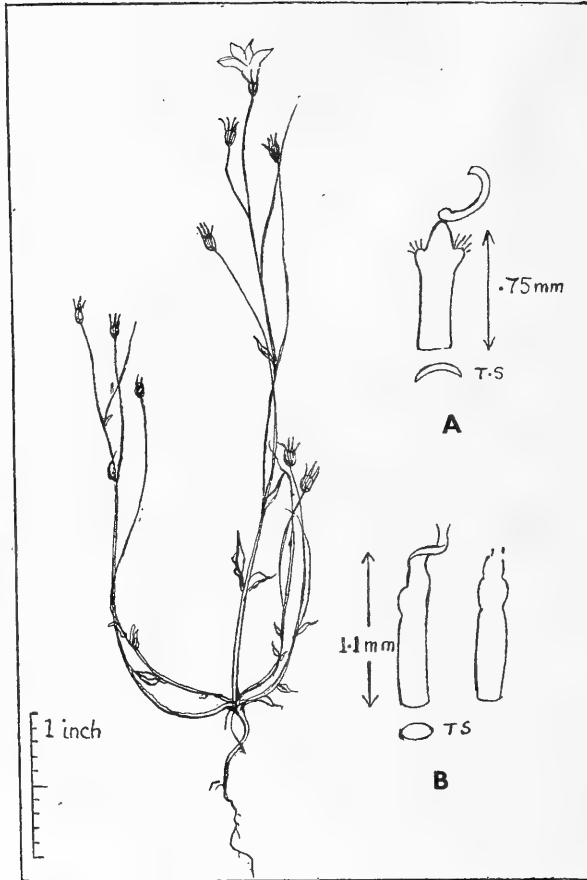


Fig. 2.—*Wahlenbergia gracilenta*, n. sp. A, *W. gracilenta*, n. sp. Anther filaments thin and transparent. B, *W. Colensoi* N. E. Brown. Anther filaments thick and opaque.

*Description*: Slender annual or ephemeral, often completing the life-cycle in 3 weeks. *Roots* short and tapering with many fibrous roots. *Stems* usually one from which branching takes place at irregular intervals or simple; 2 to 12 inches high, covered with short stiff (whitish-grey) hairs which are usually, but not always, confined to the lower half of the stem and branches, somewhat angular below, terete above, basal branches often decumbent. *Leaves* few, usually opposite below, alternate above, those on the branches much smaller than on the main stem, ovate-lanceolate to lanceolate, frequently oblong on the branches, acute, rarely obtuse, sessile,  $\frac{1}{3}$  to  $\frac{2}{3}$  inch long,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch wide; both surfaces sparsely clothed with longish white hairs; margins irregularly serrate, and somewhat recurved, very rarely thickened or greyish-white, midrib evident below, channelled above. *Peduncles* glabrous, slender, 2 to 6 inches long; *pedicels* very numerous, filiform. *Flowers* small, three- to six-lobed, blue to white. *Calyx* three- to five-lobed, rarely more,  $\frac{1}{8}$  to  $\frac{1}{6}$  inch, erect, broad subulate, acute to sub-acute, tube (ovary) ovoid, glabrous, as are the calyx lobes. *Corolla* three- to six-

lobed (usually appearing on the same plant), small,  $\frac{1}{10}$  to  $\frac{3}{16}$  inch in diameter,  $\frac{1}{12}$  to  $\frac{1}{8}$  inch long, lobes spreading, ovate-lanceolate, acute, tube slightly longer than the calyx lobes. *Style* well exerted from the mouth of the corolla tube with two to four stigmatic lobes at its apex. *Stamens* three to six, slightly shorter than the style, slender with narrow ligulate non-ciliate filaments. *Capsule* sub-globose to ovoid, rarely obconic,  $\frac{1}{16}$  to  $\frac{1}{8}$  inch long, rarely more than  $\frac{1}{8}$  inch in width, glabrous, prominently marked with vertical lines, usually half as many again as the calyx lobes; valves two to four, protruding above the rim of the capsule to a third the length of the calyx lobes, two- to four-celled. *Seeds* variable in number, minute, light brown, compressed, ovoid.

*Habitat*: Especially common in most coastal heathlands and dwarf-scrubs, where overhead covering is limited. It prefers sandy or gravelly formations to heavier soils.

*Discussion*: It is this species more than any other which has been wrongly determined as *W. gracilis*. Its habit differs from all the previously described species, and although the above description includes many ephemeral forms, in addition to those of more robust and branching nature, these could be segregated only after a most careful and thorough examination has been made, not only of all available material, but also of the climatic characteristics of the locality.

The percentage of three- to six-lobed calyces and corollas frequently increases as the flowering period proceeds. It is not rare on a well-developed plant to find all possible combinations between these variations. This may account for this species having been erroneously referred to as *W. quadrifida* (R.Br.) A.D.C., many recent authors failing to appreciate specific distinctions of that plant.

Although geographical separation precludes confusion in the field, it is possible that with dried material confusion may occur with the New Zealand species, *W. Colensoi* N. E. Brown. Although in depauperated states the two species appear identical, *W. gracilentia* lacks the basal multiple branching and tufted habit, obovate to oblanceolate leaves, ciliated filaments and the much smaller flowers and fruits of that species. It is the author's contention that *W. Colensoi* N. E. Brown belongs to the *W. marginata* (Thunb.) A.D.C. complex and is not related to the Australian Continental type.

#### WAHLENBERGIA SIEBERI A.D.C.

*Monogr. Camp.*, 1830, 144.

#### *Synonymy.*

*Campanula Sieberi* D. Dietrich, *Syn. Pl.*, i, 1834, 753.

The TYPE of this species was collected by Sieber, and is labelled "Nova Hollandia, no. 577". The type material is preserved in de Candolle's Herbarium at the Conservatory of the Botanic Gardens, University of Geneva, Switzerland.

Despite records by J. M. Black for this species in South Australia, up to the present, no fresh or dried material examined can be identified with this species, and this may be due to the following reasons:

(a). Essential diagnostic details (on present-day standards) not contained in the original description.

(b). Insufficient details discernible from the photograph of Sieber's type.

(c). No actual comparison of recently-collected material with the type, which may be referable to another species when better understood.

#### *Description*.\*

"*W. caule ramosa basi dense hispido, foliis subdenticulatis acutis, inferioribus lanceolato-obovatis, pilosis, superioribus linear-lanceolatis glabriusculis, calyce glabro, tubo ovoideo, corolla tubulosa lobis calycinis fere triplo majore, capsula obovoidea.*

Campanulaceae, Sieb. fl. Nov. Holl. n 577.

Habitat in Nova Hollandia.

Radix tenuis albidā, fibrosa, pollicaris. Caulis erectis, à basi ramosus 8 pollices altis; per inferiorem partem angulosus, foliosus, et dense hispidus, pilis albis subretroarsis rigidis. Folia alterna, margine alba cartilaginea, undulata, semidentata, acuta ima

\* This description is given in its original form.

lanceolata obovata, 6 lineas longas, 2 lin. lata, pilosa, alia lineari lanceolata paulo majora glabriuscula. Pedunculi nudiusculi, in pedicellos filiformes 3-6 lineas longos subdivisi. Flores numero 9 in nostra specimine, subpaniculati alabastra nutantia. Calyx glabra per anthesin sesquilineam, longus, tubo ovoidea; lobis linearibus, angustis erectis tubo brevioribus. Corolla (ex spec. herb. Kunth.) caerulea, circiter  $2\frac{1}{2}$  lineas longa tubulosa, superne 5 loba, lobis patentibus. Stamina lineam longa. Stylus longitudine tubi corollae exnumero loculamentorum in aliis speciminibus. Capsula obovoidea, erecta, 2 lineas longa, teres lobis calycinis erectis desinens, 3 locularis, apice 3 valvis dehiscens. Semina minutissima, ovoidea, nitida.

Specimine nostrum floribus caret, sed aliud ejusdem originis, in herb. Kunthiano vidi. Species *W. gracilis* affinis, sed forsam *W. dehiscenti* adhuc propior. Differ à priori, caule basi angulata, foliis paulo latioribus quam vulgo, foliis. *C. marginatae* Thunb. (jap. pl. dec. 3) similibus, caule et foliis basi dense hispidis, pilis rigidis, inflorescentia subracemosa, pedunculis subdivisis, lobis calycinis premissis, angustis, stricte linearibus; corolla parva, tubulosa 5 loba, non vero 5 fida. *A. W. dehiscenti* sequentibus notis differt, caule basi angulosa, pilosissimo; foliis brevioribus, pilosis, marginatis, majis acutis, capsula paulo brevior, lobis calycinis post anthesin non incurvatis sed solum erectis."

#### WAHLENBERGIA CAPENSIS A.DC.

*Monogr. Camp.*, 1830, 136, t. 18. Gardiner, *Census of W. Aust. Plants*, 1931, p. 123. *Synonymy.*

*Campanula capensis* Linn., *Sp. Pl.*, 1753, 169; *Mem. acad. Peterb.*, 4, 374, t. 6, Fig. 3; *Bot. Mag.*, t. 782. *Campanula elongata* Willd., *Enum. Herb. Berol.*, Suppl., 10. *Roella decurrens* Andr., *Bot. Rep.*, t. 238; non l'Her. *Wahlenbergia elongata* Schrad., *Cat. Hort. Goett.*, 1814.

*Distribution:* Native to Cape Colony, where it is widespread. It has now become naturalized in certain parts of south-west Western Australia, notably in and about Perth. It appeared first in that State about 30 years ago.

*Description:* Strong growing annual, with stems 12-18 inches high, usually erect, simple or branched, hairy at the base. *Leaves* often opposite on the lower part of the stem, ovate-lanceolate or lanceolate, 1 inch to  $2\frac{1}{4}$  inches long,  $\frac{1}{2}$  to  $\frac{3}{4}$  inch wide, pilose, irregularly toothed and often lobed. *Peduncles* elongated, one-flowered glabrous or scabrid. *Flowers* at first drooping, but at length nearly erect. Broad-campanulate, usually less than  $\frac{3}{4}$  inch diameter. *Calyx* covered with recurved white hairs, lobes 5, linear-lanceolate,  $\frac{1}{4}$  inch long, tube (ovary)  $\frac{1}{4}$  inch long, hirsute. *Corolla* twice the length of the calyx, bluish-green on the outside, dark blue on inside, frequently spotted with black; lobes 5, ovate-lanceolate, violaceous in colour. *Stamens* 5, filaments not examined. *Style* exerted beyond the mouth of the corolla tube, with 3 stigmatic lobes at the top. *Capsule* obovoid,  $\frac{1}{3}$  to  $\frac{1}{2}$  inch long, up to  $\frac{1}{4}$  inch wide, hirsute. *Seeds* ovoid, numerous, pale brown.

*Discussion:* In appearance it is totally distinct from any species endemic to Australia. Its allies appear to be the *vincaeflora* group, but none of the species belonging to this group are sufficiently close to cause confusion between this and the endemic species. Apart from morphological characters, the geographical separation prevents this. I am indebted to Miss M. Teede, of Perth, for a very fine series of specimens of this species.

#### WAHLENBERGIA VINCAEFLOA (Vent.) Decne. Fig. 3.

*Rev. Hort.*, 1849, Ser. iii, p. 41, cum fig.; *Gard. Mag. Bot.*, 1851; *Paxton's Fl. Gard.*, ii, 1851, 13, Fig. 142; *Fl. Cab.*, 1851; Irving in *Gard. Chron.*, liv, 1912, 216; N. E. Brown in *Gard Chron.*, liv, 1913, 357, pro parte.

*Synonymy.*

*Campanula vincaeflora* Vent., *Jard. Mal.*, 1803, t. 12; Poiret, *Encycl. Meth.*, 1811, Suppl. ii, 56—excluding all varieties. *Campanula gracilis*, *Bot. Mag.*, t. 691; W. Aiton, *Hortus Kewensis*, 1810, 2nd Ed., 344 (possibly). *Campanula gracilis* var. *vincaeflora*

Roem. et Schult., *Syst.*, v, 1819, 97, pro parte. *Wahlenbergia gracilis* var.  $\alpha$  A.DC., *Monogr. Camp.*, 1830, 142, pro parte. *Wahlenbergia gracilis* var. *littoralis* A.DC., *Monogr. Camp.*, 1830, 142; G. Don, *Gen. Syst.*, iii, 1834, 739; DC., *Prod.*, vii, 1837, 433. *Wahlenbergia marginata* var. *littoralis* Hochreutiner in *Candollea*, v, 1934, 29. *Wahlenbergia gracilis* Sulman, *Wild Fl. N.S.W.*, ii, 124, Pl. xliii.

*Distribution*: New South Wales, and probably limited to that State, where it appears to be widely spread on the east coast. It may possibly occur on the eastern side of Victoria or south-east Queensland.



Fig. 3.—*Wahlenbergia vincaeflora* (Vent.) Decne. Partly opened flower.

At present, the existence of type material is unknown to the author, either in England or on the Continent. As the plant Decaisne described, as well as Ventenat, was garden grown, the lack of type material is not surprising. For both plants all that exists are plates, which for exactness are not all that could be desired, Decaisne's plant being a colour sketch only. A provisional NEOTYPE has, therefore, been selected from material recently collected in New South Wales by F. M. Hilton (Coll. No. 448) found in the vicinity of Ingleburn, where it is common amongst scrub. This NEOTYPE has been lodged in the National Herbarium, Melbourne. Another specimen collected in the same locality (Hilton, No. 447) has been placed in the National Herbarium, Sydney, as a TOPOTYPE. The following is a complete list of areas from which this species is at present recorded: *New South Wales*: Michelago, "G.B.", Jan., 1887, (S); Jennings, J. H. Maiden and J. L. Boorman, Dec., 1903, (S); Molong, J. Boorman, Nov., 1906, (S); Dalmorton, E. Cheel, Nov., 1914, (S); The Valley, Hornsby, W. F. Blakely,

Oct., 1915, (S); Cola, 6 miles from Hill Top, E. Cheel, 22 Oct., 1916, (S); Tuena, J. Boorman, Nov., 1918, (S); Ingleburn, F. Hilton, Nos. 431, 449, 452-4, Oct., 1943, (L); Parramatta, no date, no coll., (M); Richmond River, C. Fawcett, no date, (M). *Queensland*: (Although two localities are here quoted, further material is needed to ascertain the correctness of these determinations.) Taylor Range, near Brisbane, 800-1,000 ft., rocky slope amongst *Eucalyptus*, C. E. Hubbard, No. 3748, 24 Aug., 1930, (B); Gympie, Dr. F. H. Kenny, July (?), (B).

*Extended Description*: *Rootstock* fleshy, penetrating deeply into the substrate, frequently branching. *Stems* indefinite in number, arising from the apex of the rootstock, simple, rarely branching, erect but often decumbent at the base, 9 to 24 inches high, scabrid for their entire length, somewhat angular and striated below, terete above. *Leaves* restricted to the lower third of the stem, usually opposite below, alternate above, sessile and somewhat decurrent,  $\frac{1}{2}$  inch to 2 inches long, and up to  $\frac{1}{4}$  inch wide, lanceolate to linear-lanceolate, rarely linear or ovate, scabrid on both surfaces especially along the midrib on the under surface, margins serrate, undulate, often beset with hairs, upper leaves usually minutely and remotely denticulate. *Peduncles and pedicels* terete and scabrid, almost destitute of cauline leaves. *Calyx* of 5 erect, attenuate, scabrid lobes, extending, when in bud, well beyond the corolla and equal in length to corolla tube when in flower,  $\frac{2}{3}$  to  $\frac{1}{2}$  inch long, medial vein prominent; tube (ovary) hemispherical with 5 to 10 prominent vertical veins, covered with stiff hairs, frequently with tubercles at their bases. *Corolla* 1 inch to 1 $\frac{1}{4}$  inches in diameter, frequently whitish or pale on the outside, azure-blue inside; lobes 5, spreading lanceolate-ovate, acute,  $\frac{3}{8}$  inch in length, usually marked with 1 to 3 prominent veins; tube equal to length of the lobes, goblet-shaped, deep yellow in colour. *Stamens* 5, large and inserted at the base of the corolla tube, filaments widening at their tops into a hairy trilobed and recurving membrane, terminating with a very slender white connective. *Style* slender, longer than the corolla tube, simple below but splitting into 3 slender stigmatic lobes, 2 to 3 mm. long. *Capsule* hemispherical or sub-globose,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch long, up to  $\frac{1}{8}$  inch wide, covered with stiff hairs, frequently with tubercles at their bases, prominently ribbed; valves three, protruding above the rim of the capsule. *Seeds* minute, numerous, shiny and of a pale brown colour, ovoid to oval.

*Discussion*: Limited to the above description, which is based on the original, *W. vincaeflora* differs from all other large-flowered species in the following characteristics:

- i. All vegetative parts are covered by stiff short whitish hairs.
- ii. The tube of the corolla is sulphur yellow.
- iii. The calyx tube and capsule are hemispherical.
- iv. The outside of the corolla is frequently whitish.

The delineation of *Campanula vincaeflora* Ventenat varies from that of Decaisne in several respects, but as this was made from cultivated plants, such variation can be expected. The present writer considers that both Ventenat's and Decaisne's plants are from the same seed stock, which, grown under artificial conditions, would possibly produce differences from the original plant (which the writer believes is identical with Hilton's collections). As both descriptions refer to the capsule being "semi-globular and pubescent" and "calyx pubescent" the identity of these plants is apparent. The most likely source of seed for such an introduction is the neighbourhood of Port Jackson, where *W. vincaeflora* is still common. The related *W. consimilis* appears to be limited in its distribution to Victoria and South Australia, and certain areas in south-western New South Wales.

Because of the early introduction of seed into England and the Continent, it is probable that most of the references to *Wahlenbergia* in horticultural literature refer to this very beautiful plant. It is impossible from such references accurately to refer to one species or another, but taking into account the small details which are given, and the only possible source of seed at this date, it would appear safe to refer most of them to this species.



R. Brown's variety of *Campanula gracilis*, namely, var. *vincaeflora*, is referable to *W. quadrifida* (R.Br.) A.D.C., and is in no way connected to the above species. Hooker's variety of *Wahlenbergia gracilis*, namely, var. *vincaeflora*, as defined in his "Flora of Tasmania", covers several plants, none of which is identical with the above species, many of his collectings being referable to *W. gymnoclada*, n. sp., as well as to other species.

It would appear from N. E. Brown's description that the above distinctions were not appreciated, and J. M. Black has perpetuated this error. Until experimental and field work had been completed the writer was not fully aware that certain characteristics were specific.

The size and colouring of the blooms, produced freely over a long period, render both *W. vincaeflora* and *W. consimilis* worthy of inclusion in any rock garden, and attention has already been drawn to their popularity in European gardens for more than a century.

#### WAHLENBERGIA CONSIMILIS, n. sp.

Affinis *W. vincaeflorae* forma et statura, sed distincta caulibus rigidis, erectis (20-60 cm. alta, raro 80 cm.), hirsutis, supra glabrescentibus, foliis lanceolatis, 1-5 cm. longis, 0.5-1.0 cm. latis, dense pubescentibus, marginibus crispatis; calyce attenuato, glabroso; corollae lobis ovatis, acutis, tuba urceolata; capsula glabrosa, lata, obconica, 1.0 cm. longa, 0.75 cm. lata; seminibus multis.

References have been made to this species under the name of *W. vincaeflora* in the following publications: *Paxton's Flower Garden*, iii, 1852, 33, Fig. 137; "W.T.", *Gard. Chron.*, liv, 1912, 216 and illus.; N. E. Brown, *Gard. Chron.*, liv, 1913, 355. References are also made to this species under the name of *W. gracilis* var. *littoralis* in the following publications: A DC., *Monogr. Camp.*, 1830, 144, pro parte; G. Don, *Gen. Syst.*, iii, 1834, 73; DC., *Prod.*, vii, 1837, 433, pro parte. Mention is also made to it under the name of *W. gentianoides* in *Gard. Chron.*, 1912, 216; in Obs. on R.H.S. Show.

*Distribution*: *Victoria*: Warby Ranges, NE. Vict., savannah, amongst granitic outcrops, 20 Sept., 1942, N. Lothian, TYPE, Aust. Felix, F. v. Muell., Dec., 1848, (M); Dandenong Rgs., Chas. Walter, Nov., 1896, (S); Preston, no coll., 1899, (M); Cambelfield, P. R. H. St. John, 2 Nov., 1900, (M); Diggers Rest, P. R. H. St. John, 6 Nov., 1901, (M); Hawkesdale, H. B. Williamson, Nov., 1902, (S); Pakenham, P. R. H. St. John, 26 Nov., 1904, (M); Ferntree Gully, A. J. Tadgell, Oct., 1934, (T); Altona, P. R. H. St. John, 24 Nov., 1906, (M); Eltham, P. R. H. St. John, Sept., 1927, (B); Bendigo, "Kangaroo Flat", A. J. Tadgell, Oct., 1934, (T); Upper Buckland Valley, 2,000 ft., Rev. J. P. Oates, Jan., 1938, (T); Sunshine, Kelior Plains, A. J. Tadgell, 21 Oct., 1938, (T); St. Albans, Kelior Plains, J. H. Willis, 22 Nov., 1941, (M); Ararat, Miss L. L. Banfield, 3 Nov., 1941, (L); Stawell, Miss L. L. Banfield, 13 Nov., 1941, (L); Dandenong Rgs., Ferny Ck., J. H. Willis, 11 Jan., 1942, (M); Mornington Peninsula, J. H. Willis, 18 Jan., 1942, (M); Macedon, main road to Hump, P. Bibby, Feb., 1943, (L); Warrandyte, N. Lothian, 21 Nov., 1943, (L). *New South Wales*: Gulgong, ? James, 1879, (M); Leath, L. Abrahams, Sept., 1910, (S); Temora, Rev. W. Dwyer, No. 7535/14, Oct., 1914, (S); Warrenbane, P. F. Morris, Oct., 1935, (M); Albury, N. Lothian, Nov., 1940, (L); between Darling and Lachlan Rrs., Burkett, no date, (M); Albury, H. Beatie, no date, (M). *Queensland*: Moreton district, Stradbroke I., C. T. White, Sept., 1913 ?, (B). *Tasmania*: Hobart, A. H. S. Lucas, Dec., 1923, (S). *South Australia*: Rapid Bay, R. Tate, Nov., 1877, (A); Ardrossan, J. B. Cleland ?, Nov., 1879, (A); Monarte Sound, J. B. Cleland, 16 Oct., 1923, (C); Mt. Remarkable, J. B. Cleland, 8 Nov., 1926, (C); Mt. Gambia, Miss C. E. Eardley, Nos. 2426-7, 19 Oct., 1935, (W); Hallett's Cove, J. B. Cleland, 16 Nov., 1930, (C); Hallett's Cove, J. B. Cleland, 28 Nov., 1933, (C); Morialto, J. B. Cleland, Dec., 1934, (C); National Park, J. B. Cleland, 16 Dec., 1929, 11 Nov., 1934, 20 Oct., 1935, 12 Nov., 1938, (C); Belair, Miss C. E. Eardley, No. 1970, 5 Oct., 1929, (W); Beaumont Rd., Waterfall Gully, J. B. Cleland, 12 Oct., 1935, (C); Waitfira, no coll., 26 Jan., 1936, (M); Cut Hill, Encounter Bay, J. B. Cleland, 5 Dec., 1936, (C); Torrens River, F. v. Muell., no date, (M); Mt. Lofty Ranges, no coll., no date, ("monptrapitas"),

(M); Mt. Lofty Ranges, Jas. Addison, no date, (B). *Western Australia*: Darling Range, A. H. S. Lucas, Oct., 1928, (S).

*Description*: *Rootstock* perennial, thick and fleshy, frequently branching, penetrating deeply. *Stems* usually many to a plant—rarely one, simple or branching at the base, erect, sometimes decumbent at the base, 8 to 24 inches high, rarely up to 30 inches, more or less angular below and covered with long white hairs, becoming glabrous and terete above. *Leaves* confined to the lower half of the plant, opposite or alternate, closely placed, or rarely as a basal rosette, sessile and usually decurrent. Basal leaves frequently ovate to spatulate, others lanceolate to linear lanceolate, rarely linear,  $\frac{1}{2}$  inch to 2 inches long, up to  $\frac{1}{2}$  inch wide, covered on both surfaces by long whitish hairs, coriaceous, margins thickened, crispate, rarely flat and dentate, midrib channelled above, prominent below; cauline leaves few, linear and slightly pubescent. *Peduncles* usually long, branching, glabrous. *Flowers* large, dark blue in colour, whitish or pale on exterior, calyx lobes often reflexed when corolla expanded. *Calyx* 5 sepals, rarely 4 to 7, narrow deltoid or attenuate,  $\frac{3}{8}$  to  $\frac{5}{8}$  inch long, glabrous, equal to or slightly longer than the corolla tube; tube (ovary) ovoid, glabrous, and usually veined. *Corolla* normally 5 petals, but frequently 4 to 8, rarely more, up to  $1\frac{1}{2}$  inches in diameter, lobes spreading, ovate, acute,  $\frac{5}{8}$  inch long, up to  $\frac{3}{8}$  inch wide, medial vein prominent, tube  $\frac{1}{4}$  to  $\frac{1}{2}$  inch long, usually white or pale interior. *Stamens* 5, filaments large, with two prominent wings, edged with long hairs. *Style* simple, slightly longer than the corolla tube, with two prominent collars, one just below the base of the stigmatic lobes, the other half-way down the style; stigmas 3 to 4 mm. long, and recurving. *Capsule* barrel-shaped or sub-globose, glabrous,  $\frac{1}{4}$  to  $\frac{1}{5}$  inch long, up to  $\frac{1}{4}$  inch diameter, prominently ribbed, two-thirds the length of the calyx lobes, which surmount the capsule; valves 3, nipple-shaped before opening, extending well above the rim of the capsule. *Seeds* numerous, oval, brown.

*Habitat*: Common in the drier parts of south and south-western New South Wales, also Victoria and South Australia, usually in areas in which savannah conditions obtain. Material collected from Queensland, Tasmania and Western Australia should be treated with reserve.

*Discussion*: Included previously with *W. vincaeflora* (Vent.) Dcne., from which it differs by its glabrous calyx, lobes and capsule, pale throat and barrel-shaped capsule; it is hoped that the description of this and the preceding species will clear up two of the most confusing plants yet encountered. The habitat of the two species is different, and while specimens of the above species have been noted with pubescent calyx and capsule, this variation is extremely rare.

At present there appears to be a montane form of this species, found growing at the Dandenong Ranges, Victoria, and other similar areas in the southern part of that State, which diverges from the typically coriaceous plant. Not only is it smaller in all its parts—flowers rarely exceed  $\frac{3}{4}$  inch in diameter—but the foliage is almost glabrous on the upper surface. This may possibly be a distinct variety, but evidence at present is not conclusive, especially as this form is only known from damp areas, where conditions are conducive to such variations. It has been noted that plants under cultivation continue to present such variations.

As yet no material of both this and the preceding species has been collected in the same area. This supports the view that, while *W. consimilis* favours open plain or savannah conditions of a dry nature, *W. vincaeflora* prefers areas where rainfall is not only more abundant but soil conditions favour better growth.

WAHLENBERGIA GLORIOSA, n. sp.

Planta, perennis, 10–40 cm. alta; caulibus gracilibus, infra hirsutis, supra glabrosis; foliis saepe oppositis, ovatis vel elliptico-lanceolatis, 0.5–3.5 cm. longis, 0.4–0.8 cm. latis, coriaceis superiore lamina glabra, inferiore hirsutis; marginibus spissatis, crispatis, raro dentatis; pedunculis longis gracilibus, glabrosis; calyce glabroso, 0.2–0.4 cm. longo, lineari, deltoideo, acuto; corolla azurea vel purpura, magna, 1.75–2.8 cm. lata, tuba lobis

aequa; filamentis ligulatis; stylo longissimo, stigmatibus bi-lobis, 1 mm. longis, capsula obconica, 0.4–0.7 cm. longa, 0.3 cm. lata; seminibus minutis, multis.

*Distribution:* *Victoria:* Mt. Buffalo, P. R. H. St. John ?, March, 1930, TYPE, (M); Mt. Hotham, Chas. Walter, Jan., 1899, (M); Mt. St. Bernard, H. B. Williamson, Jan., 1908, (M); between Harrietteville and Mt. St. Bernard, 5,100 ft., A. J. Tadgell, March, 1935, (T); between Mts. Hotham and Feathertop, 6,000 ft., A. J. Tadgell, Dec., 1914, et Dec., 1922, (L); Mt. Bogong, 6,000 ft., A. J. Tadgell, Feb., 1923, (L); between Towonga and Mt. Fainter, "The Springs", 5,000 ft., A. J. Tadgell, Jan., 1928, (L); towards Mt. Nelson, 5,700 ft., A. J. Tadgell, Feb., 1930, (L); Mt. Buffalo, rocky approaches to Lake Catani, J. H. Willis, Jan., 1938, (M); Mt. Buffalo, W. Boys, May, 1942, (M); Mt. Torbreck, 5,000 ft., grassy places between rocks, J. H. Willis, March, 1943, (M). *New South Wales:* Katoomba, Federal Pass, approx. 2,500 ft., Dixon, Aug., 1904, (S); Tamworth, Kosciusko, Pilliga Scrub, J. B. Cleland, 10 Dec., 1910, Gudgenbenby, Queanbeyan, R. H. Cambage, No. 3294, 14 Jan., 1912, (S); Mt. Kosciusko, "Brett's Camp", J. H. Maiden, Feb., 1914, (S); Kosciusko district, E. Harnett, Nos. 712/21, Feb., 1921 (white form), (S); Kosciusko district, Mrs. Messmer, 1940, (S); Barrington Tops, sub-alpine grasslands, 4,800 ft., C. T. White, No. 11507, 26 March, 1938, (B); Barrington Tops, Dungog, J. L. Boorman, no date, (S).

*Description:* *Rootstock* perennial, penetrating deeply into the substrate, fleshy. *Stems* usually several per plant, slender, erect, frequently decumbent at the base, simple, rarely branching, lower half covered by long white hairs; somewhat angular, becoming glabrous and terete above. *Leaves* confined to the lower half of the plant, opposite, rarely alternate, decussate, or rarely as a loose rosette; lower leaves flaccid or subcartilaginous, ovate to oblanceolate,  $\frac{3}{4}$  to  $\frac{1}{2}$  inch long, up to  $\frac{3}{8}$  inch wide, upper surface glabrous, under surface pubescent, but hairs usually confined to the midrib, margins somewhat thickened, undulate, dentate rarely entire; upper leaves sub-cartilaginous, oblong-lanceolate, rarely linear, acute,  $\frac{1}{2}$  inch to  $1\frac{1}{2}$  inches long, up to  $\frac{1}{3}$  inch wide, glabrous, rarely pubescent and then limited to the midrib on the under surface, margins cartilaginous recurved, crispate, rarely serrate; midrib obscure above, rarely channelled, prominent below, lateral veins obscure above, apparent below. *Peduncles* slender, long and glabrous, one per stem, usually unbranched. *Flowers* deep blue to royal purple, throat rarely differing in colour from the lobes, up to  $1\frac{1}{4}$  inches in diameter. *Corolla* tube shorter than the lobes. *Calyx* 5 sepals, erect, glabrous,  $\frac{1}{10}$  to  $\frac{1}{8}$  inch long, narrow deltoid, acute, half the length of the corolla tube, lengthening as the capsule matures; tube (ovary) glabrous, broad obconic. *Corolla* 5 petals, lobes spreading, lanceolate to ovate-lanceolate, acute prominently veined,  $\frac{3}{8}$  inch to  $1\frac{1}{4}$  inches in diameter; tube shorter than the lobes, wide mouth, tapering sharply to narrow base,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch long, rarely differing in colour from the lobes. *Stamens* 5, anthers equal to the length of the corolla tube, filaments broad ligulate, with two small shoulders, pilose on the edges only. *Style* long and slender, sharply contracted for about three-quarters of its length, densely pubescent when mature, extending well beyond the mouth of the corolla tube, stigmatic lobes 2 to 3, ovate, 1 mm. long, rarely recurving. *Capsule* glabrous, broad obconic,  $\frac{1}{8}$  to  $\frac{3}{10}$  inch long, up to  $\frac{3}{10}$  inch wide, surmounted by 5 erect calyx lobes, almost equalling the length of the capsule, prominently ribbed, valves 2 to 3, protruding slightly above the rim of the capsule, loculi 2 to 3. *Seeds* minute, dark brown, glossy.

*Habitat:* Grassy places between boulders, on mountain tops, usually at and above 5,000 ft.

*Discussion:* It differs from *W. vincaeflora* (Vent.) Dcne. (with which it has been previously included) in the glabrous calyx and capsule, ovate lanceolate leaves and shortened stigmatic lobes; and from *W. consimilis*, n. sp., it can be easily separated by its foliage, single slender stems, colour of the corolla and the shorter calyx lobes.

It is a most remarkable as well as beautiful species. The stigmatic lobes are unusually short, as well as being bilobed in numerous specimens, and the filaments, instead of being large and lobed, are simple in shape, broad ligulate in outline, and the appendages reduced to two small shoulders, instead of the glandular pilose wings

which are normally associated with the large-flowered group. A form at variance with the typical has been collected at Mt. Hotham (Walter), Kosciusko (Messmer), and Queanbeyan (Cambage). The foliage in these specimens is usually closely set, decussate pairs, and frequently hirsute on both surfaces. This is no doubt an ecological form and what little experimental work has been carried out on the above species tends to show that, along with many others, it is easily affected by changed environmental conditions. Another variation from the typical has been collected from Barrington Tops. In this the leaves are flaccid, almost totally glabrous, rarely with recurved edges, and the capsule is somewhat larger than in the type. This may eventually prove to be distinct, but until further material has been collected and more is known about its habit, the safer course would be inclusion with the above species. *W. gloriosa* is a distinctive alpine species, being indigenous only to areas above 4,500 ft. It bears some resemblance to the New Zealand *W. albo-marginata* Hk. f., but the rosette habit of that species is entirely absent. As its name implies, it is a superb plant, worthy of cultivation, as are *W. vincaeflora* and *W. consimilis*.

In addition to the mentioned forms of *W. gloriosa*, material has been collected from alpine regions which is totally distinct and at present appears to be an undescribed species. Possessing lanceolate-linear leaves and smaller flowers than the above, it should be kept apart in all future collections. Until this has been done and its habit fully known, further identification is impossible.

#### WAHLENBERGIA BILLARDIERI, new name.

##### *Synonymy.*

*Campanula littoralis* Labill. in *Nov. Holl.*, 1809, t. 70; Poiret, *Encycl. Meth.*, ii, 1816, 56, pro parte. *C. gracilis* var. *littoralis* R.Br., *Prod.*, 1810, 561.

*Distribution:* Probably confined to coastal and light forest areas in Victoria and Tasmania. Its range at present is not known, but collections by the writer have been made at the following Victorian localities: Torquay, among *Lepidosperma*, *Burchardia*, *Dianelia* and *Hibbertia* on sandy soil, open, with no top cover, Oct., 1943; Warrandyte, north bank of the River Yarra, amongst *Eucalyptus polyanthemos*, with little supporting ground vegetation, Nov., 1943; Heathmont, savannah, *Eucalyptus obliqua*, etc., with light ground vegetation, clay soil (Silurian), Nov., 1941.

*Emended Description:* Perennial, 9 to 15 inches high. *Rootstock* thick and fleshy, whitish. *Stems* erect, slender, one per plant, rarely more than three, 6-15 inches high, simple, seldom branching, lower part angular and beset with short stiff hairs, gradually becoming glabrous and terete above. *Leaves* confined to the lower half of the stem, opposite and decussate in distant pairs, very rarely alternate, ovate to lanceolate,  $\frac{1}{4}$  to 1 inch long, up to  $\frac{3}{8}$  inch wide, sessile, seldom decurrent, almost glabrous on the upper surface, hirsute below, rarely with whitish setae, or almost glabrous, midrib channelled above, prominent below, margins somewhat recurved, hardly thickened, crispate, rarely dentate, entire or flat. *Peduncles* and *pedicels* glabrous, slender. *Flowers* medium size, blue to pale mauve and white, corolla tube goblet-shaped, with corolla and calyx segments frequently varying in number. *Calyx* 5 sepals, frequently varying from 4 to 6, erect, narrow deltoid, glabrous,  $\frac{1}{8}$  to  $\frac{1}{6}$  inch long, almost equal to the length of the corolla tube; tube (ovary) broad obconic to sub-globose, glabrous. *Corolla* 5 petals, rarely 4 to 6,  $\frac{1}{2}$  to  $\frac{3}{4}$  inch in diameter, lobes spreading, ovate lanceolate, acute,  $\frac{1}{4}$  to  $\frac{3}{8}$  inch long, tube frequently yellow or more often white; almost equal in length to corolla lobes, goblet-shaped. *Stamens* 5, filaments roughly deltoid, with small shoulders, entirely covered with glandular hairs. *Style* slender, well extended beyond the corolla tube, with three (rarely 2 or 4) slender stigmatic lobes, 3 mm. long at the apex. *Capsule* glabrous,  $\frac{1}{4}$  to  $\frac{1}{2}$  inch long,  $\frac{1}{8}$  inch wide, slightly longer than the calyx lobes, ribbed but not prominently so, valves three, opening level with the rim of the capsule. *Seeds* minute, brown and ovoid.

*Discussion:* There is a sheet of material in de Candolle's Herbarium at Geneva, labelled "*Campanula littoralis*", collected by Gaudichaud at Port Jackson in 1804. This sheet is referable to *W. vincaeflora* (Vent.) Dene., if only on account of the corolla

lobes. On the same sheet is a single specimen comprising a single stem, with opposite ovate leaves, devoid of all flowering parts, which may be referred to *W. Billardieri*. In view of this, a provisional NEOTYPE has been selected. This material was collected by Robert Brown at Arthur's Seat, Port Phillip, Victoria, in 1804, and is preserved at the British Museum (Natural History), South Kensington, England.

Together with this material, and mounted on the same sheet, is another specimen of R. Brown's, labelled "*Campanula gracilis* v. *littoralis*, Prod. 561, TYPE 2617". This is also referable to the present species. A further specimen is also mounted on the same sheet, and was collected by Lhotzky "pique Sydney at Port Jackson 1838", this being, at present, an undescribed species. At the base of this sheet is the inscription "*W. vincaeflora* (Dcne.) N. E. Brown".

While agreeing in the main with the emended description, the plate in Labillardier's "Plantae Nova Holland" differs from the above, possibly due to artistic licence, which often affected botanical drawings of the early nineteenth century. The detailed dissections of the floral parts are almost identical. The growth habit depicted shows variation in the length of the foliage, which the writer considers may be referable to the form growing in light forest at Heathmont and Warrandyte.

Schlechter and Brehmer (*Engl. Jahrbuch*, liii, 1915, 127) described a South African species as *W. littoralis*, and as Article 61 of the International Rules of Botanical Nomenclature invalidates a later homonym, I have renamed this species after its original describer, who first gave it specific rank.

#### WAHLENBERGIA GYMNOCLADA, n. sp.

*Planta* perennis, gracilis, paene glabrosa, 20–30 cm. alta; foliis ad basim laxa rosetta restrictis, linearibus, paene glabrosis, 2–6 cm. longis, 0.3 cm. latis; pedunculis, longissimis, raro ramosis, unifloris; corolla 1.5–2.0 cm. diametra, lobis duplo-longioribus tuba; capsula obconica, 0.4–0.7 cm. longa, 0.25–0.3 lata; seminibus multis.

*Discussion*: In the past, this species has been included with *W. vincaeflora* (Vent.) Dcne., from which it differs in its almost glabrous condition, linear leaves, short corolla tube and calyx lobes, and elongated obconic capsule. It may also be confused with *W. quadrifida* (R.Br.) A.DC., from which it differs in its larger corolla, well-formed corolla tube, longer peduncles, and growth habit.

*Rootstock* perennial, thin, frequently branching. *Stems* usually one to many per rootstock, 9 to 15 inches high, frequently single, more often 2 to 6 and only branching at the base, erect or somewhat decumbent at the base, where sparsely hairy; glabrous and terete above. *Leaves* confined to the basal part of the plant as a loose rosette, rarely scattered along the stems, and then opposite or rarely alternate; decurrent, entirely glabrous or a few scattered hairs, on the under surface, then only on the midrib and base of lamina; linear, rarely lanceolate, spreading, rarely adpressed,  $\frac{3}{4}$  inch to 2 inches long,  $\frac{1}{8}$  to  $\frac{1}{2}$  inch wide, margins somewhat thickened, entire or serrate, often minutely so, slightly recurved; cauline leaves scattered and few, alternate or opposite, linear, glabrous,  $\frac{3}{4}$  to 1 inch long,  $\frac{1}{12}$  to  $\frac{1}{10}$  inch wide, margins remotely and minutely dentate, slightly recurved. *Flowers* borne singly on long slender peduncles, 4 to 10 inches long, with one or two cauline bracts, blue to purple, rarely white,  $\frac{3}{4}$  inch to 1 $\frac{1}{4}$  inches in diameter, calyx lobes shorter than corolla in bud. *Calyx* 5 sepals, glabrous,  $\frac{1}{8}$  to  $\frac{3}{16}$  inch long, narrow deltoid, acute or sub-acute, equal to corolla tube or slightly exceeding it, medial vein prominent; tube (ovary) obconic, glabrous, equal to calyx lobes, frequently ribbed. *Corolla* 5 petals, with at least one prominent vein per petal,  $\frac{3}{4}$  inch to 1 $\frac{1}{4}$  inches in diameter,  $\frac{3}{4}$  inch long; lobes ascending spreading,  $\frac{3}{16}$  to  $\frac{5}{16}$  inch long,  $\frac{1}{10}$  to  $\frac{1}{8}$  inch wide, tube short, two-thirds the length of the corolla lobes. *Stamens* 5, filaments broad ligulate, shoulders not prominent, hairs just obvious. *Style* simple, napiform exerted well above the rim of corolla tube, branching at the apex into 3 stigmatic recurving lobes, 2 mm. long. *Capsule* obconic, glabrous, stout, ribbed,  $\frac{3}{16}$  inch wide,  $\frac{1}{4}$  to  $\frac{3}{16}$  inch long, approximately twice the length of the calyx lobes; valves 3 at apex, protruding well above the rim of the capsule. *Seeds* numerous, ovoid-oval, shining brown.

*Habitat*: Open country bordering the coast, but not littoral.

*Synonymy*.

*Wahlenbergia gracilis* var. *vincaeflora* Hook. f., *Fl. Tasm.*, 1860, 239. *W. vincaeflora* var. *littoralis* N. E. Brown, *Gard. Chron.*, liv, 1913. *W. gracilis* var. *littoralis* A.D.C., *Monogr. Camp.*, 1830, 144; G. Don, *Gen. Syst.*, iii, 1834, 73; DC., *Prod.*, vii, 1837, 433. *Campanula littoralis* Poiret, *Encycl. Meth.*, ii, 1816, 56, No. 72, pro parte.

*Distribution*: The TYPE, from Gorae West, near Portland, Victoria, was collected by C. Beauglehole and lodged in the National Herbarium, Melbourne.

The species is known only from Victoria and Tasmania at the present time, from the following localities: *Victoria*: Frankston, P. St. John, 14 Dec., 1905, white-flowered form, (M); Ringwood, amongst light forest, N. Lothian, Oct., 1935, (Cairns & L); Welspool, between Pt. Albert and Wonthaggi, almost on sea coast plains, A. J. Tadgell, 31 Oct., 1938, (L); Clarinda, heathlands, on sandy areas, little overhead growth, N. Lothian, 12 Nov., 1941, (L); Bemm River (E. Victoria), Miss Wigan, Dec., 1941, (L); Gorae West, near Portland, on open and lightly forested areas, C. Beauglehole, Nov., 1943, TOPOTYPE, (L); Wilson's Promontory, Musgrani, no date, (M). *Tasmania*: New Norfolk, Macquarie, Gunn, No. 72/1842, 19 Nov., 1842, pro parte, (S); Cape Portland, Miss Brandinct, 1884, (M); "Tasmania", Dr. Storey, no date, (M); "α tasmaniae", Dr. J. D. Hooker, no date, ex Muell. Herb., (M).

Several specimens were examined in the Gunn Herbarium, now preserved in the National Herbarium, Sydney, and beyond the label stating the collection was made by Archer, little information as to the exact localities was obtained.

WAHLENBERGIA TADGELLII, n. sp.

Planta perennis, 25–60 cm. alta; caulibus rigidis, erectis, glabrosis, a basi hirsutis; foliis ad basim caulium positis, linearibus lanceolatis inferiore lamina et marginibus paulo pubescentibus, 3–6 cm. longis, 0.2–0.5 cm. latis; marginibus integris vel denticulatis; pedunculis rigidis; floribus caeruleis, 0.75–1.25 cm. latis, corolla 5 lobata, lobis expansis tubis brevis, capsula lata et conica; 0.9–1.25 cm. longa, 0.5 lata.

*Rootstock* perennial, thick, usually branching. *Stems* one to many arising from a common base, 12 to 24 inches high, erect or slightly decumbent at the base; rigid, simple or rarely branching, and then at the base only; longish hairs on the basal parts, frequently angular, becoming glabrous and terete above. *Leaves* usually confined to the lower part of the plant, alternate or sub-opposite, spatulate-lanceolate to lanceolate or linear, acute, 1 inch to 2½ inches long, ¼ to ⅓ inch wide, sessile, decurrent, upper surfaces glabrous, rarely with scattered hairs, under surface with scattered hairs confined to the midrib, less frequently on the margins; margins entire or denticulate, and then remotely so, slightly undulate, thickened and often recurved, midrib obvious above, prominent below, lateral nerves obscure. *Peduncles* rigid, but often slender, glabrous, frequently branching above. *Flowers* rarely more than ⅓ inch diameter, usually 5-petalled, but polypetalous occurring, deep blue, white throat. *Calyx* 5–6 sepals, glabrous, narrow deltoid, acute, erect, ½ to ⅓ inch long, 2 to 3 times the length of the corolla tube, medial vein obscure. *Corolla* 5-lobed, blue, up to ⅓ inch in diameter, lobes ovate lanceolate and spreading, tube rarely more than one-fifth the length of the lobes, wide mouth usually with white or yellow base. *Stamens* 5, filaments broad ligulate, 1 mm. long, 1 mm. broad, with two erect ciliate shoulders. *Style* well exerted beyond the mouth of the corolla tube, almost filiform below, three broad stigmatic lobes at the apex. *Capsule* glabrous, broad obconic, with 10 vertical ribs, frequently obscure when green, prominent when dry, usually with indentations just below the rim of the capsule, large and stout, ½ to ⅓ inch long, up to ¼ inch in diameter, frequently three times the length of the calyx lobes; valves three, protruding for half the length of the calyx lobes above the rim of the capsule. *Seeds* large, 0.75 mm., ovoid oblong, compressed, dark brown when mature.

*Habitat*: Sporadic but widespread in Victoria on heathlands etc., also in New South Wales and South Australia, where it should be sought in savannah.

*Distribution:* *Victoria:* Elsternwick, "among grass and other low vegetation", 200 ft., A. J. Tadgell, Oct., 1938 (affin.), (L); Grampians, Miss L. L. Banfield, 13 Nov., 1941, (L); Stawell, along railway line, Miss L. L. Banfield, 13 Nov., 1941, (L); Doncaster, savannah, under *Eucalyptus melliodora*, with *Themadra* sp., N. Lothian, Nov., 1943, (L); Torquay, sandy soil, growing amongst *Lepidosperma*, *Carex*, *Dillwynia* and low herbaceous plants, TYPE, N. Lothian, Nov., 1943, (L); Ararat, Charl Green, No. 119, no date, (M). *New South Wales:* Warrembane, P. F. Morris, 1935, (M). *South Australia:* Bugle Range, F. v. Muell., Oct., 1845, (M).

*Discussion:* A distinct species, easily identified by its strong-growing, erect and rigid stems, sometimes up to 2 feet high, almost glabrous linear-lanceolate leaves, medium size corolla with short tube, and stout capsule.

Its nearest ally appears to be *W. quadrifida* (R.Br.) A.DC., from which it is distinguished by the above characters, especially that of the capsule, which in *W. quadrifida* is elongate-obconic. Most of the material examined is homogeneous, although slight variation does occur. Several sheets of material collected at Yarra Junction, Victoria, show extreme variation in foliage, and it is possible that we are again dealing with a polymorphic species, which is also easily affected by ecological conditions. These collections have been held in abeyance until finality can be reached.

The species has been named in honour of A. J. Tadgell, a veteran botanist and collector, in appreciation of the very great kindnesses which I have received from him at all times, more especially during work on the present genus, and in admiration of his numerous botanical writings.

#### WAHLENBERGIA MULTICAULIS Benth.

Hugel, *Enum. Pl. Nov. Holl.*, 1837, 75; N. E. Brown, *Gard. Chron.*, liv, 1913, 337, excluding var. "dispar".

*Distribution:* Western Australia. The TYPE was collected by Hugel on the banks of the Swan River, and is preserved in the Herbarium of the University of Göttingen. Beyond the type collection, and a fragment in the Kew Herbarium (which may be from the type specimen), the present writer has seen only one other specimen, viz., W. Drummond, No. 425, National Herbarium, Melbourne, which is identical with the type. It is not known where this specimen was collected.

*Description:* Entirely glabrous perennial plant, 10 to 12 inches high, with many stems and erect slender branches. *Rootstock* unknown. *Stems* slender, many, arising from the top of rootstock, simple or branching below, glabrous, erect, very rarely decumbent at the base, 10 to 12 inches high, terete, slightly ribbed. *Leaves* numerous, absent only from the peduncles, linear, acute, glabrous,  $\frac{3}{8}$  inch to  $1\frac{1}{2}$  inches long, rarely more than  $\frac{1}{12}$  inch wide (lower differing only in size from the upper); margins cartilaginous, entire or denticulate, undulate, midrib prominent beneath. *Flowers*, colour not known. *Calyx* glabrous, narrow and short deltoid,  $\frac{1}{2}$  to  $\frac{3}{8}$  inch long, 2 to 3 times the length of the corolla tube; tube (ovary) glabrous, obconic, two-thirds the length of the calyx lobes. *Corolla*  $\frac{1}{2}$  to  $\frac{3}{4}$  inch in diameter, lobes spreading, lanceolate,  $\frac{3}{16}$  inch long, tube short,  $\frac{1}{16}$  inch long. *Stamens* 5, almost equalling the length of the corolla lobes, filaments, medium size, with ciliate and somewhat incurved edges. *Style* exerted beyond the corolla tube, with 3 stigmatic lobes at its apex. *Capsule* glabrous, obconic,  $\frac{3}{8}$  inch long,  $\frac{1}{10}$  inch wide (rarely elongate-obconic, except when totally desiccated), almost equal to the persisting calyx lobes; valves 3, protruding one-third the length of the calyx lobes above the rim of the capsule. *Seeds* minute, numerous,  $0.5 \times 0.25$  mm.

*Discussion:* This species was confused previously with any of the "multicauleate" group, but principally *W. bicolor* and *W. quadrifida*; it differs from the former by its totally glabrous habit, linear leaves and short corolla tube, while from *W. quadrifida* it is easily separated by its larger flowers, totally glabrous habit and linear leaves.

Its distribution is very limited and local; over 50 sheets of Western Australian material have afforded very few specimens approaching this species. This is all the

more strange when we recall that this species is the only one so far recorded from Western Australia!

The exact position of the South Australian material is not yet finalized, as specimens resembling both *W. multicaulis* and *W. bicolor* have been collected from that State. The effect of environmental conditions has not as yet been fully explained, and it appears unwise to give a decision until all relevant factors have been fully considered.

WAHLENBERGIA BICOLOR, n. sp. Fig. 4.

*Synonymy.*

*Campanula gracilis* var. *stricta* R.Br., *Prod.*, 1810, 561. *Wahlenbergia gracilis* var. *stricta* Roem. et Schult., *Syst.*, v, 1819, 97; A.D.C., *Monogr. Camp.*, 1830, 142; G. Don, *Gen. Syst.*, vii, 2, 1834, 433.

*Distribution:* *New South Wales:* Port Jackson, environs, R. Brown, Oct.-Nov., 1803; Parramatta, ex Muell. Herb., no. coll., no date, (M); Minori, J. L. Boorman, No. 2/99, (S); Guyra, Chandler's Peak, J. L. Boorman, March, 1917, (S); Marthaguy Shire, no coll., July, 1935. *Victoria:* Port Phillip, Arthur's Seat, R. Brown, May, 1802, LECTOTYPE, (BM); Dargo Flat, Nos. 61, 65, Howitt, 1882, (M); Aust. Felix, F. v. Muell., no date, (M); Government Domain, near Melbourne, J. Minchin, no date, (M); Somerton, P. St. John, 1 May, 1903, (M); Bacchus Marsh, J. R. Tovey, 3 Nov., 1910, (M); Werribee, P. St. John, Oct., 1921, (M); Eltham, P. St. John, Oct., 1926, (M); Diamond Ck., No. 5, P. St. John, Sept., 1927; between St. Albans and Sydenham, A. J. Tadgell, 24 March, 1934, (M); Bacchus Marsh, A. Miebald, No. 21845, Dec., 1936,



Fig. 4.—*Wahlenbergia bicolor*, n. sp.



(M); Kelior Plains, A. J. Tadgell, Sept.-Dec., 1937-39, (L); Elsternwick, sandy soil, amongst grass, A. J. Tadgell, May, 1930 and 1939, (L); Newport, grasslands, F. S. Colliver, Oct., 1938, (L); Culgoa, Mrs. F. S. Barton, 1938, (L); Sandringham, heath scrub, A. J. Tadgell, Oct., 1938, (L); Garfield railway station, J. Galbraith, 25 April, 1939, (L); Mansfield, Phosphate Hill, F. S. Colliver, 1942, (L); Warby Ranges, NW. of Wangaratta, savannah, granitic soils, N. Lothian, Oct.-Nov., 1942, (L); Lorne, high mountain behind township, P. F. Morris, Feb., 1943, (L); Creswick, J. H. Willis, Jan., 1944, (M); Torquay, amongst grass on golf course, N. Lothian, Oct., 1943, (L); Werribee, no coll., no date, (M); Grampians, near Station Peak, no coll., no date, (M). *South Australia*: St. Vincent's Gulf, F. v. Muell., 1851, (M); Bugle Range, F. v. Muell., Nov., 1878, (M); Georgetown, Mrs. A. F. Richards, 1893, (C); Encounter Bay, J. B. Cleland, Feb., 1935, May, 1939, (C); Beaumont Road to Waterfall Gully, J. B. Cleland, 12 Oct., 1935, (C); Morialto, J. B. Cleland, 5 Oct., 1935, 3 Jan., 1936, (C); Hallett (Cove?), J. B. Cleland, 16 Nov., 1938, (C); Brookerly, J. B. Cleland ?, no date, (C).

*Description*: Much-branched perennial plant, glabrous except for scabrid hairs about the basal parts. *Rootstock* thick, perennial, fleshy with deep penetrating branches. *Stems* many, 6 to 50 cm. high, erect and frequently rigid, rarely lax or decumbent at their bases, sometimes short and tufted, totally glabrous, except for the basal portions, which are usually covered with short scabrid hairs, rarely striated. *Leaves* numerous and scattered, almost glabrous, linear to lanceolate, rarely ovate-lanceolate, acute,  $\frac{2}{3}$  inch to  $1\frac{1}{4}$  inches long, rarely more than  $\frac{1}{2}$  inch wide; margins denticulate or rarely entire, frequently recurved, midrib channelled above, prominent below (both these features becoming more obvious in herbarium material). *Peduncles* slender and graceful, but frequently short, glabrous. *Flowers* produced in abundance, medium size, azure-blue inside, frequently white, yellow or old gold on the outside of the corolla, polypetalous occurring to a greater extent than observed in any other species. *Calyx* 5 sepals, erect (rarely 6 to 10), glabrous, narrow deltoid, acute,  $\frac{1}{2}$  inch long; quarter as long again as the corolla tube; tube (ovary) glabrous, elongated obconic. *Corolla* 5 petals (6- to 18-petaled specimens rarely occurring), up to  $\frac{3}{4}$  inch in diameter, corolla tube open,  $\frac{3}{8}$  inch long, frequently whitish towards the base, one-third the length of the corolla, lobes ovate-lanceolate, spreading,  $\frac{2}{3}$  inch long,  $\frac{1}{2}$  inch wide, azure-blue inside, pale yellow or white on the outside. *Stamens* 5 (frequently aborting and fragmentary or absent in polypetalous specimens), filaments broad, triangular with two ciliate incurved shoulders. *Style* slender, well exerted from the mouth of the corolla tube, stigmatic lobes 3, half the length of the style. *Capsule* slender, elongate, glabrous, up to  $\frac{5}{8}$  inch long, up to  $\frac{1}{2}$  inch wide, prominently veined; valves three, protruding well above the rim of the capsule. *Seeds* numerous, very small, pale to dark brown.

*Habitat*: Favouring savannah and dry open formations, e.g., lava plains of western Victoria, and open savannah in South Australia and New South Wales.

*Discussion*: Material of this species was extensively collected by Robert Brown from the regions around Port Jackson and from Port Phillip.

It is material from the latter locality which has been chosen as the LECTOTYPE, and this material is preserved in the British Museum (Natural History), England. There are three collections mounted on the same sheet as the lectotype, which is the central specimen and at the top bears a label "type specimen", while at the base is one of R. Brown's "Iter Australiensis" labels, "no. 2617, *Campanula* c, Port Phillip 1802 May" (The other two collections are labelled *Campanula simplicicaulis* and *Campanula gracilis*  $\alpha$  respectively.)

*W. bicolor* is clearly distinct from *W. multicaulis* Benth., with which it has previously been included.

There are at least two forms commonly collected:

(a). Typical, which is found in most Victorian areas and coastal regions of New South Wales, especially in heavily grassed plains and savannah country. It has also been collected in South Australia.

(b). Short tufted and compact plant which possesses numerous erect unbranched peduncles. This form may be considered as a variety (or even species) after further investigation. It prefers dry open areas, with little competing vegetation, and has been collected from the basaltic Kelior Plains (southern Victoria) and localities in north-western Victoria (Ni Ni Well and Glenlee).

Although originally described as *Campanula gracilis* var. *stricta* R.Br., use of the varietal epithet is precluded by the existence of *W. stricta* Sw. (referable to the *W. gracilis* complex), hence this species has been renamed *W. bicolor* on account of the contrasting pale or yellow colour usually manifest on the outside of the corolla. This species is constant in all features described, except for the colour variation of the corolla.

In passing, mention should be made of the galls which are frequently seen on collected and growing material. At times such material shows variation from the typical, and as it rarely bears perfect flowers identification is difficult. Another manifestation of insect attack is to be found on plants, tufted in habit with ovate-lanceolate leaves, set on short sterile stems.

#### WAHLENBERGIA SAXICOLA A.DC.

*Monogr. Camp.*, 1830, 144; G. Don, *Gen. Syst.*, iii, 1834, 740, No. 20; *J. Linn. Soc. Lond.*, ii, 1858, 21; in obs.; Hook. f., *Fl. Tasm.*, i, 1860, 239, t. lxxi, A 1-6; Benth., *Fl. Aust.*, iv, 1869, 138; Tasm. plant only; W. Irving, *Gard. Chron.*, lii, 1912, 216, pro parte; N. E. Brown, *Gard. Chron.*, liv, 1913, 354; L. H. Bailey in *Cycl. Hort.*, iii, 1937, 3495.

#### *Synonymy.*

*Campanula saxicola* R.Br., *Prod.* 1810, 561, et l.c., 1821; Poiret, *Encycl. Meth.*, ii, 1811, 58, No. 78; Roem. et Schult., *Syst.*, v, 1819, 898; Spreng., *Syst.*, i, 1825, 736; D. Dietrich, *Syn. Pl.*, i, 1839, 753. *Streleskia montana* Hook. in *Lond. J.*, vi, 1841, 267.

*Distribution: Tasmania:* TYPE collected at Mt. Wellington, at the summit, (BM); Diamond Springs, Mt. Wellington, A. Simson, 27 March, 1878, (M); Middlesex Plains (south of Ulverston on north coast, C. S. Sutton, Jan., 1911, (M); "Tasmania", no date, ex Archer's Herbarium, (S); "Top of Mt. Wellington", A. Simson, no date (portion of above collection?), (Q).

*Description:* *Rootstock* perennial, white and fleshy. *Stems* herbaceous and, in favoured positions, numerous, rarely erect, usually prostrate, glabrous or with few scattered hairs. *Leaves* 6 to 18 in number, in tight rosette, more rarely on short stems or elongated axis,  $\frac{3}{4}$  to 1 inch in diameter, sessile, lanceolate to spatulate, obovate or oblanceolate,  $\frac{3}{8}$  to 1 inch long,  $\frac{1}{10}$  to  $\frac{1}{4}$  inch wide, usually entirely glabrous, or with few scattered hairs, margins unthickened, irregularly and slightly toothed, midrib on under side prominent, venation otherwise obscure, but reticulate when visible. *Peduncles* rarely more than 1 per rosette, 1 to 4 inches high, glabrous and erect, slender, prominently lined, usually without cauline bracts. *Flowers* smallish, clear blue in colour, up to  $\frac{1}{2}$  inch in diameter. *Calyx* 5-lobed, rarely 3- or 4-lobed, glabrous,  $\frac{1}{8}$  to  $\frac{1}{12}$  inch wide, up to  $\frac{1}{10}$  inch long, linear lanceolate, acute, tube (ovary) sub-globose. *Corolla* 5-lobed, campanulate,  $\frac{1}{4}$  to  $\frac{1}{2}$  inch in diameter, tube short,  $\frac{1}{10}$  inch long, lobes  $\frac{3}{8}$  to  $\frac{1}{8}$  inch long, up to  $\frac{1}{10}$  inch broad, oblong lanceolate, acute. *Stamens* 5, often irregular in shape. *Style* two-thirds the length of the corolla. *Stigma* 3-lobed. *Capsule* globose, rarely sub-globose, glabrous,  $\frac{1}{2}$  to  $\frac{3}{4}$  inch long, up to  $\frac{1}{4}$  inch in diameter, prominently marked with vertical veins, 3-valved. *Seeds* shining, light brown, oblong ovoid.

*Discussion:* Until the publication of N. E. Brown's paper, this species had been repeatedly confused with the New Zealand *W. albo-marginata* Hk. f., on what grounds it is hard to understand. Its low growing habit, glabrous and slightly toothed lanceolate-spatulate leaves and globose capsule distinguish it from that species, while its constantly single-flowered peduncles, together with the above characteristics, separate it from any other Australian species.

## XIII. WAHLENBERGIA OF LORD HOWE ISLAND.

Species of *Wahlenbergia* indigenous to Lord Howe Island have previously been described under *W. gracilis* A.DC., and the first island check-list to mention the above species is Mueller's,\* published in 1875. Subsequently it has appeared in local floras compiled by Hemsley,† Tate,‡ Oliver,\*\* and others.

Lord Howe Island is noted for the high degree of endemism among its plants and their affinity with those of New Zealand. This character is well exemplified by the species described below, for not only are the flowers akin to the New Zealand species, but the general growth habit—leaves, capsules, etc. (in both the caespitose and tall-growing species), exhibits this affinity. It may be possible, with further information, to show that the caespitose species were evolved from the same stock as the New Zealand and Tasmanian. The close relationship between the New Zealand and Lord Howe Island sub-fruticose forms is at once apparent, while such types from Tasmania are, for the most part, referable to continental Australia rather than to New Zealand.††

It is possible that plant migration into the island is still taking place. In *Wahlenbergia* one extra-Australian and two native species have already appeared in mainland localities far removed from their original range. Observations made with one of our indigenous species, *W. quadrifida* (R.Br.) A.DC., indicated that this species can quickly adjust itself to new conditions and because of its perennial rootstock obtain a permanent foothold and eventually become part of that flora; a similar position has arisen in regard to *W. capensis* A.DC., the South African species which is now naturalized in and about Perth.

With the above examples in mind, except for specimens already in herbaria, either in Australia or overseas, all subsequent collections evincing elements other than those herein described should be regarded with suspicion (as to their place in the original flora).

Of the caespitose forms found on this island, *W. limnophalyx*, n. sp., appears to be the younger, since it frequently throws out basal leaves similar to those (in shape and texture) of *W. insulae-howei*, n. sp., whereas specimens of that species show no variation whatsoever.

It is possible that this species is merely a distinct variety of *W. insulae-howei* which has become stabilized as a result of growing in exposed situations. This is supported by the variation which occurs in the upright species (as yet undescribed), some forms of which show serrated foliage, while in others the leaves are entire but undulate. Such variation may be the result of environmental conditions rather than any inherent morphological characteristics giving systematic definition.

Finality on such a question can only be reached after more material has been examined in conjunction with field observations. In any case it is extremely unlikely that the original biotype is still present on the island.

## WAHLENBERGIA LIMNOPHALYX, n. sp.

Planta caespitosa perennis, 2–6 cm. alta, caule brevi, angulata; foliis densis, acutis, lanceolatis, 0.75–1.25 cm. longis, 0.1–0.3 cm. latis; paucis hirsutis a basi, marginibus cartilagineis, saepe cinearscensibus (albis), serrulatis, crenulatis; floribus magnis, quinque-lobis; calyce quinque-lobis subulato, 0.3–0.5 cm. longo; corolla caerulea, tubae aequis; staminibus quinque; capsula lata, obconica, costata; seminibus multis.

*Rootstock* perennial, long and tortuous. Stems many per rootstock, and probably persisting perennially, glabrous, covered with decussate leaf scars; usually 1½ to 2 inches long, decumbent and branching below, forming tufted plants, but elongating

\* F. Mueller, *Fragm. Phytogr. Aust.*, ix, 1875, 77.

† W. B. Hemsley, *Ann. Bot.*, No. 38, June, 1896.

‡ R. Tate in the Macleay Memorial Volume (*Linn. Soc. N.S.W.*), 1893, 205–221.

\*\* W. R. B. Oliver, *Trans. N.Z. Inst.*, xlix, 1916, 94–101.

†† The relationship between the floras generally, of Australia, Lord Howe Island and New Zealand have been discussed by several authors, notably Tate and Oliver, op. cit.

under favourable conditions, and then 2 to 4 inches, ascending, with leaves scattered along their entire length. *Leaves* crowded on short stems in tightly packed spirals, lanceolate, rarely spatulate,  $\frac{1}{3}$  to  $\frac{2}{3}$  inch long,  $\frac{1}{8}$  to  $\frac{1}{4}$  inch wide, sessile and somewhat decurrent, margins slightly undulate, sparsely hirsute towards the axils, and on the undersides only, midrib prominent below, channelled above. Upper leaves practically glabrous. *Flowers*  $\frac{1}{4}$  to  $\frac{1}{10}$  inch long,  $\frac{2}{8}$  inch in diameter, pale lilac. *Peduncles* slender, glabrous, one or more per rosette, branching above into 1 to 4 pedicels. *Calyx* 5-lobed, glabrous, subulate,  $\frac{1}{10}$  to  $\frac{1}{8}$  inch long, one-third the length of the corolla. *Corolla* 5-lobed, funnel-shaped, lobes ascending spreading,  $\frac{2}{8}$  inch diameter,  $\frac{1}{4}$  to  $\frac{1}{10}$  inch long, lobes equal to the length of the tube. *Stamens* 5, filaments small. *Style* simple, slightly more than half the length of the corolla, with three stigmatic lobes at its apex. *Capsule* broad obconic, glabrous, ribbed,  $\frac{1}{8}$  inch in diameter,  $\frac{1}{16}$  inch long, surmounted by 5 erect calyx lobes. *Seeds* minute.

*Distribution*: TYPE, Lord Howe Island, "from North Hills forming small clusters on open rocky ridges at the top of seacliffs", 6th Nov., 1913, W. R. B. Oliver. The type is housed at the National Herbarium, Sydney. Part of the type is also located in the National Herbarium, Melbourne.

*Discussion*: Differs from the preceding in its lanceolate and serrate leaves, presence of hairs on the under surface of the petiole, larger calyx and corolla, and its broad obconic capsule.

After collecting the above species Dr. Oliver dispatched material to Kew for comparison with existing types. The material was returned with the following note: "a rather dwarfed saxicolous form of *W. albo-marginata* Hk.f.". Although showing superficial likeness to that species, its tufted creeping habit, branched pedicels and smaller flowers at once separate it. From the Tasmanian *W. saxicola* Hk.f. it also differs, in addition to the above features, in its foliage.

Despite the above differences, it resembles the *W. albo-marginata* complex rather than any species found within the continental area.

#### WAHLENBERGIA INSULAE-HOWEI, n. sp.

Planta caespitosa, glabrosa, perennis, 3-6 cm. alta, foliis multis, rosulatis, spatulatis, lanceolatis, 1.25-3.0 cm. longis, 0.2-0.5 cm. latis, cartilagineis, marginibus crassis, integris, vel prope incisuris magnis intervallis, minime dentatis, acutis; pedunculis gracilibus, 5-9 cm. altis; pedicellis filiformis; floribus caeruleis, infundibulosis; calyce quinque-lobis, glabrosis, 0.2 cm. longo subulato; corolla quinque-lobis, 0.8 cm. diametra, 0.75 cm. longa, lobis longitudini, tubae corollae aequis; capsula subglobosa, costata, 0.2 cm. longa, 0.2 cm. lata; seminibus multis.

*Rootstock* perennial, thick and fleshy. *Stems* glabrous, short, 1 to 1½ inches long, gnarled in appearance and frequently prostrate or decumbent, simple or branched, and then usually to form another rosette, covered by persisting decurrent leaf bases. *Leaves* numerous, glabrous, sessile, lanceolate-spatulate,  $\frac{1}{2}$  to 1 inch long,  $\frac{1}{10}$  to  $\frac{1}{4}$  inch wide (blade oblong-lanceolate, petiole narrow, channelled), sub-cartilaginous, margins thickened, entire or minutely notched at the apex, undulate, rarely crenulate, midrib prominent below, above obscure. *Peduncles* rarely more than 1 per rosette, glabrous and striated, usually branching, cauline bracts linear and minutely toothed, pedicels filiform. *Flowers* lilac or blue (?), calyx approximately one-third the length of the corolla. *Calyx* 5-lobed, erect, glabrous,  $\frac{1}{10}$  inch long, narrow-deltoid, slightly more than half the length of the corolla tube; tube (ovary) sub-globose. *Corolla* 5-lobed,  $\frac{1}{4}$  to  $\frac{1}{10}$  inch long,  $\frac{1}{8}$  inch diameter, funnel-shaped, lobes equal to the tube, lobes lanceolate, ascending, spreading, acute. *Stamens* 5, filaments small. *Style* simple, slightly longer than the corolla tube with three stigmatic lobes at the apex. *Capsule* glabrous,  $\frac{1}{12}$  inch diameter, sub-globose, two-thirds length of the calyx lobes; valves 3. *Seeds* minute and numerous.

*Distribution*: Limited to Lord Howe Island, where it apparently is found in many localities. Although varying greatly, it embraces the following collections: The type, Rev. W. Woolls, Aug., 1911; the exact locality and other relevant notes concerning this

species are not recorded. It is preserved in the National Herbarium, Sydney. J. H. Maiden, no locality, April, 1908, (S); no coll.; no date, No. 87, (Fitzgerald?), (M).

*Discussion:* Great variation occurs within this species. One set of material (No. 87), which possesses distinct rosettes of spatulate leaves at the base, produces stout upright stems up to 4 inches long, upon which are placed, either oppositely or alternately, glabrous lanceolate leaves with typical margins. Another collection from Lord Howe Island (Fitzgerald, 1876) possesses long weak stems up to 6 inches long with flaccid glabrous leaves,  $\frac{1}{2}$  to 1 inch in length, lanceolate in shape, with margins which are hardly thickened but minutely serrated. In the former, the inflorescence is identical with the type, while the latter differs in its peduncles being very slender and rarely branched, the calyx lobes more slender and the corolla possessing a narrow tube.

Despite these differences, the Fitzgerald plant can be placed with no other species than the above, and the differences probably are wholly due to environmental factors.

The same may be said of Maiden's plant (4/1898), which is allied to this species but differs from the type. It has been placed provisionally with this species. It is not improbable that eventually, when we know more about these species, they may be reduced to ecological forms rather than specific identities.

#### XIV. INDETERMINATA.

When this revision was started in 1935, it was hoped to deal with all Asiatic, Australian and New Zealand species, and publish the findings as one paper. Due to numerous circumstances this has been impracticable, hence the following list is appended. Although preliminary study has commenced, a great deal of work will be necessary before a complete revision can be made.

- Campanula capillaris* Lodd., *Bot. Cab.*, t. 1406.
  - C. gracilis* var. *capillaris* R. Brown, *Prod.*, 561.
  - C. Preissii* de Vries.
  - Wahlenbergia bivalvis* Merrill.
  - W. capillaris* G. Don, *Gen. Syst.*
  - W. capillaris* Sweet, *Hort. Brit.*, 3rd Ed., 1839, 419.
  - W. confusa* Perry and Merrill, *J. Arnold Arbor.*, 1941.
  - W. (?) dioica* Domin, in Diels *Bibl. Bot.*, viii, Heft 89, 1929, 1193.
  - W. eurycarpa* Domin, l.c.
  - W. gracilis* var. *capillaris* Hk.f., *Fl. Tasm.*
  - W. gracilis* var. *capillaris* A.DC.
  - W. gracilis* var. *littoralis* Hk.f., l.c.
  - W. gracilis* var. *misera* Hemsley.
  - W. gracilis* var. *polymorpha* A.DC.
  - W. gracilis* var. *vincaeflora* Hk.f., pro parte.
  - W. marginata* var. *polymorpha* Hochreutiner, in *Candollea*.
  - W. multicaulis* var. *dispar* N. E. Brown.
  - W. Sieberi* A.DC.
  - W. vincaeflora* var. *rosula* J. M. Black.
-

A NEW SPECIES OF *LONGETIA*: THE BOTANICAL IDENTITY OF THE  
 "PINK CHERRY" OF DORRIGO TIMBER-GETTERS.

By W. A. W. DE BEUZEVILLE and C. T. WHITE.

(One Text-figure.)

[Read 26th June, 1946.]

For some years past a timber from the Dorrigo Plateau, New South Wales, has been placed on the Sydney and Melbourne markets under the name of "Pink Cherry", but only recently has complete botanical material been made available which has enabled us to clear up its botanical identification. It belongs to the genus *Longetia*, as defined by Pax ('Das Pflanzenreich') and Pax and Hoffmann in their account of the Family Euphorbiaceae in the second edition of Engler and Prantl's "Die Naturlichen Pflanzenfamilien". It is with some hesitation, however, that we follow these authors in uniting *Buraevia* Baill. (New Caledonia) and *Choriophyllum* Benth. (Malaya) with *Longetia* Baill. (New Caledonia). Considering the high degree of endemism in the New Caledonia flora and its affinities with eastern Australia the geographical distribution of *Longetia* is remarkable: five species in New Caledonia, one in subtropical eastern Australia and one in Malaya. Our plant resembles in general facies the Queensland specimens of *Dissiliaria tricornis* Benth., and the one distinction between *Longetia* and *Dissiliaria*, as far as we can see, is the absence in the latter of a carunculus on the seed. *D. tricornis* Benth. is a "composite" species based on two collections, the one from Port Essington (A. Cunningham); the other from Rockingham Bay (Dallachy), and it is doubtful if they are the same. If all these genera are to be considered distinct, then our plant would come under *Buraevia*. It is very closely allied to *B. carunculata* Baill. which differs in having shorter, broader, emarginate leaves (4-7 cm. long, 3-4.5 cm. wide), glabrous male inflorescences, longer pedicels (up to 6 mm.) to the male flowers and nearly glabrous very young shoots.

We have pleasure in dedicating the species to Mr. E. H. F. Swain, Commissioner for Forests, New South Wales, in recognition of his services to Australian forestry, and, more particularly, for the strenuous efforts he has made to retain and increase the forest reserves in eastern Australia.

In the system as proposed by Pax and Hoffmann, Engler and Prantl, Vol. 19 c. (1931), our plant would be classified as follows:

Family Euphorbiaceae.

Subfamily Phyllanthoideae.

Tribe Phyllanthaeae : Subtribe Dissiliarinae.

*LONGETIA SWAINII*, n. sp. Fig. 1.

Arbor ad 40 m. alt., partibus novellis dense ferrugineo-pubescentibus, ramulis lenticellis parvis plus minusve dense obtectis. Folia opposita glabra petiolata, lanceolata, utrinque reticulata, margine undulato-crenulata, leviter incrassata vel recurvata, nervis praecipuis ca. 12 in utroque latere; lamina 7-11 cm. longa, 2-4 cm. lata; petiolus 5 mm. longus, pubescens. Flores parvi in thyrsos racemiformes 1-2 cm. longos dispositi, ramulis pedicellisque pubescentibus. Flores masculi: Sepala 4, patentia rotundata, imbricata, extus pubescentia intus pilis paucis vestita, 2 exteriora 1.5, 2 interiora 2.5 mm. diam., pedicellis ad 2 mm. longis; stamina 8, filamentis sepalis aequalibus, antheris dorsifixis extus dehiscentibus, disco in glandulos 4 diviso, ovarii rudimentum O. Flores foemini: Sepala 4, erecta, quam in mare angustiora et crassiora; ovarium in parte

superiore pilis strigosis dense vestitum, 2-loculare; stigma sessile, 2-lobum, lobis indivisis leviter papillois; ovula in loculis gemina. Capsula oblongo-ovoidea, ca. 1 cm. longa, 2-locularis, loculis abortu 1-spermis, exocarpio crustaceo in valvis 4 solubili; semina ab apice placentae centralis liberae pendula, plano-convexa vel latere interiore leviter concavo et canaliculo centrali notato, ad apicem carunculo flavo magno multifido-pectinato ornata, testa nitida castanea.

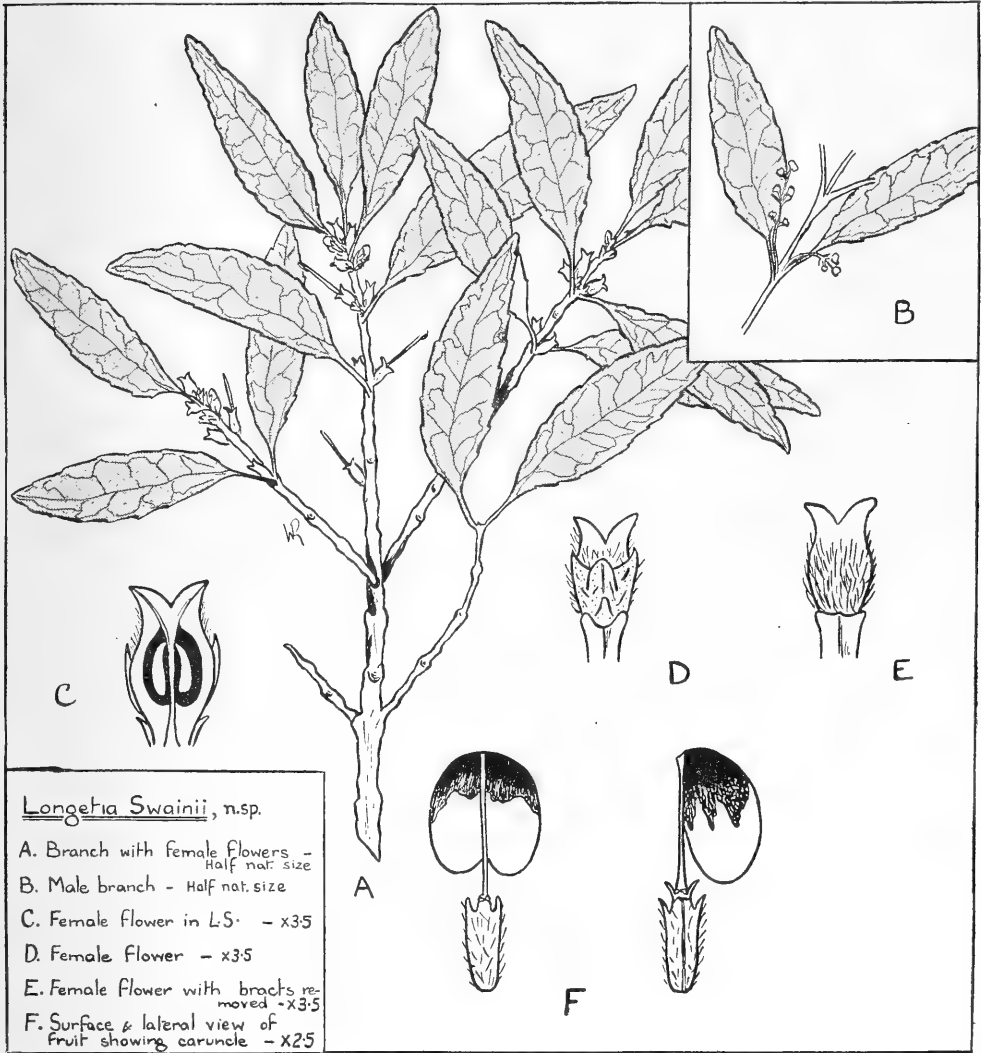


Fig. 1.

Tree up to 120 ft. high and 14 ft. girth, 4 ft. from ground, bark white and grey mottled, often scaly and peeling in small flakes, leaving circular depressions reminding one of Brown Bolly Wood or Bolly Gum (*Litsea reticulata*); very bitter. Branchlets at first densely rusty, pubescent, at length glabrous and clothed with a grey bark with numerous small lenticels. Sapwood white, timber red, like that of Rose Alder (*Ackama paniculosa*), but heavier. Leaves dark glossy green, opposite, glabrous, petiolate, lanceolate, plainly reticulate on both sides in the dried state, midrib yellow, secondary nerves and some of the net veins visible on both sides in the living leaf; margin undulate-crenate; principal nerves about 12 on each side of the midrib; blade 2-4¼ in.

long,  $\frac{3}{4}$ – $1\frac{3}{8}$  in. wide; petiole  $\frac{1}{4}$  in. long, pubescent. Flowers small, arranged in a raceme-like thyrse,  $\frac{1}{2}$ – $\frac{3}{4}$  in. long; branches and pedicels pubescent. Male flowers: sepals 4, spreading, rotund, imbricate, outer face pubescent, inner face clothed with a few hairs, the two outer ones  $\frac{1}{16}$  in., the two inner ones  $\frac{1}{10}$  in. diam., pedicels up to one-twelfth inch long. Stamens 8, filaments equalling the sepals, anthers dorsifixed, dehiscent outwards; disk divided into four glands; rudimentary ovary absent. Female flowers: sepals 4, erect, somewhat narrower and thicker than in the males; ovary densely clothed in the upper part with strigose hairs, 2-locular, stigma sessile, bilobed, lobes undivided, slightly papillose, ovules 2 in each loculus. Capsule oblong ovoid, not quite  $\frac{1}{2}$  in. long, 2-celled, each cell 1-seeded by abortion; pericarp crustaceous shed in 4 valves; seeds pendulous from the free central placenta, plano-convex or the inner face slightly concave and marked by a central groove, crowned at the apex by a large conspicuous orange-yellow, very much divided, almost lacy, caruncle; testa dark brown, shining.

New South Wales: East Dorrigo: plentiful in brush. Miss Rosling (type: male and female flowers—Herbarium, University of Sydney), March, 1944 (tree 120 ft. high, 17 in. diam., 4 ft. from ground; wood used in place of Coachwood—*Ceratopetalum apetalum*—seeds hang on trees for over a year after fruits have fallen). East Dorrigo: W. A. W. de Beuzeville (fruits), February, 1940. Dorrigo: common. Jas. A. R. King (fruits), March, 1946 (large tree). Dorrigo: G. H. Hewitt (fruits), March, 1946 (National Herbarium, Sydney). Bellingen: R. B. Rickerby (male flowers), March, 1940 (National Herbarium, Sydney). Head of Wilson's Creek, via Murwillumbah: H. Hayes (male flowers), June, 1944. Whian Whian State Forest: moderately common in rain forest. C. T. White, 12785 (male flowers), June, 1945 (tree 20 m. high, 0.5 m. diam., bark brown, rather scaly in the older trees, blaze a deep pink, leaves dark glossy green above, paler beneath; flowers greenish-yellow).

#### NOTES ON THE TIMBER.

The fine-textured timber is deep pink-brown in colour, with lighter orange-brown sapwood. The sapwood is quite well defined and relatively narrow. The solitary vessels are uniformly distributed, with a slight tendency to radial arrangement. Under the lens parenchyma is not conspicuous—microscopic examination shows it to be generally diffuse, with a little surrounding the vessels. The rays are fine and darker than the remainder of the wood—they are conspicuous on the radial surface of the timber.

This timber has been classified under the "Universal Index to Wood", compiled by Mr. E. H. F. Swain, Commissioner for Forests, New South Wales, after whom this species was named. The Index numbers are 9.22432 and 9.22424.

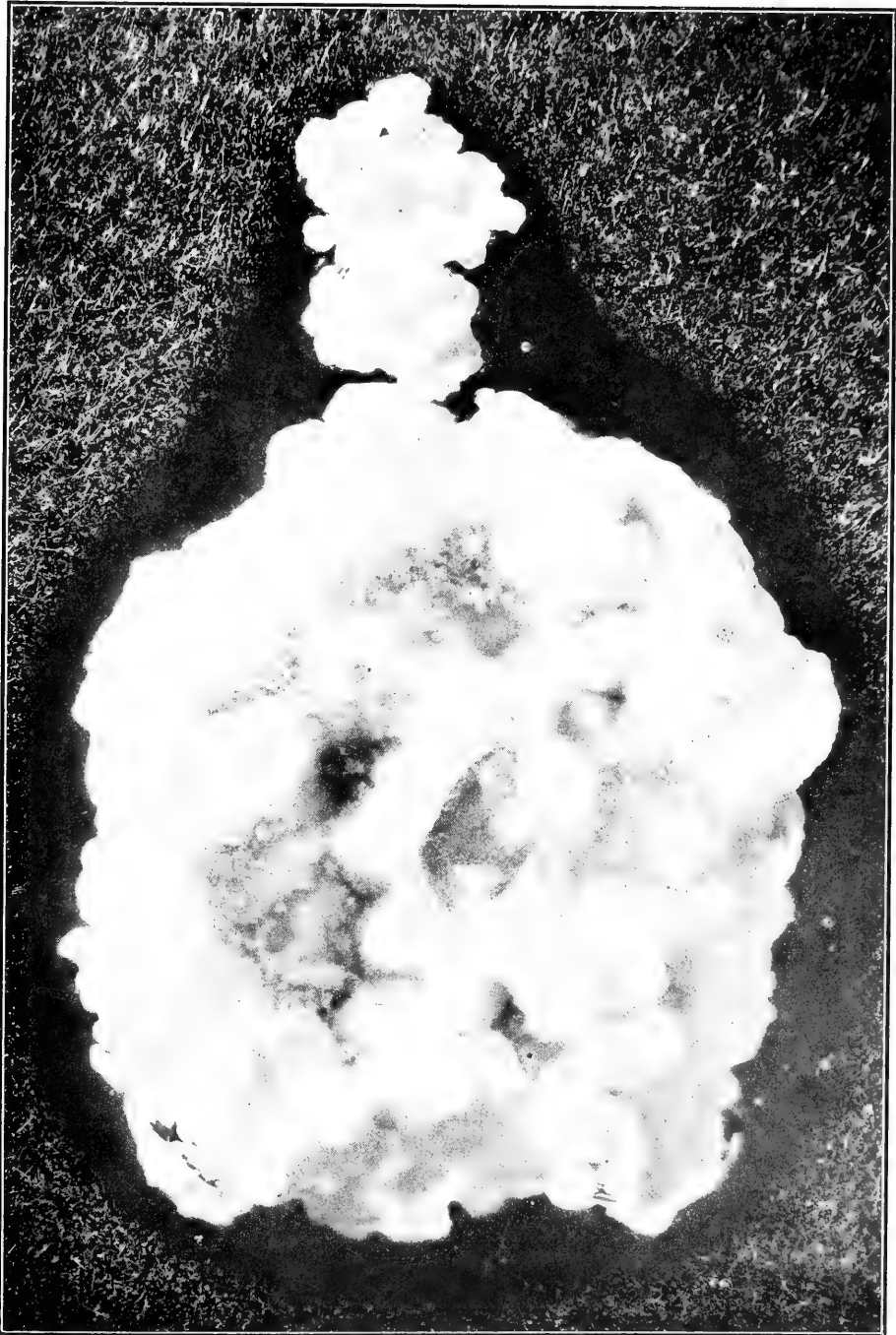
#### ACKNOWLEDGEMENT.

The authors desire to thank Miss Rosling of the Division of Wood Technology, Forestry Commission, New South Wales, for the drawings included in this paper.



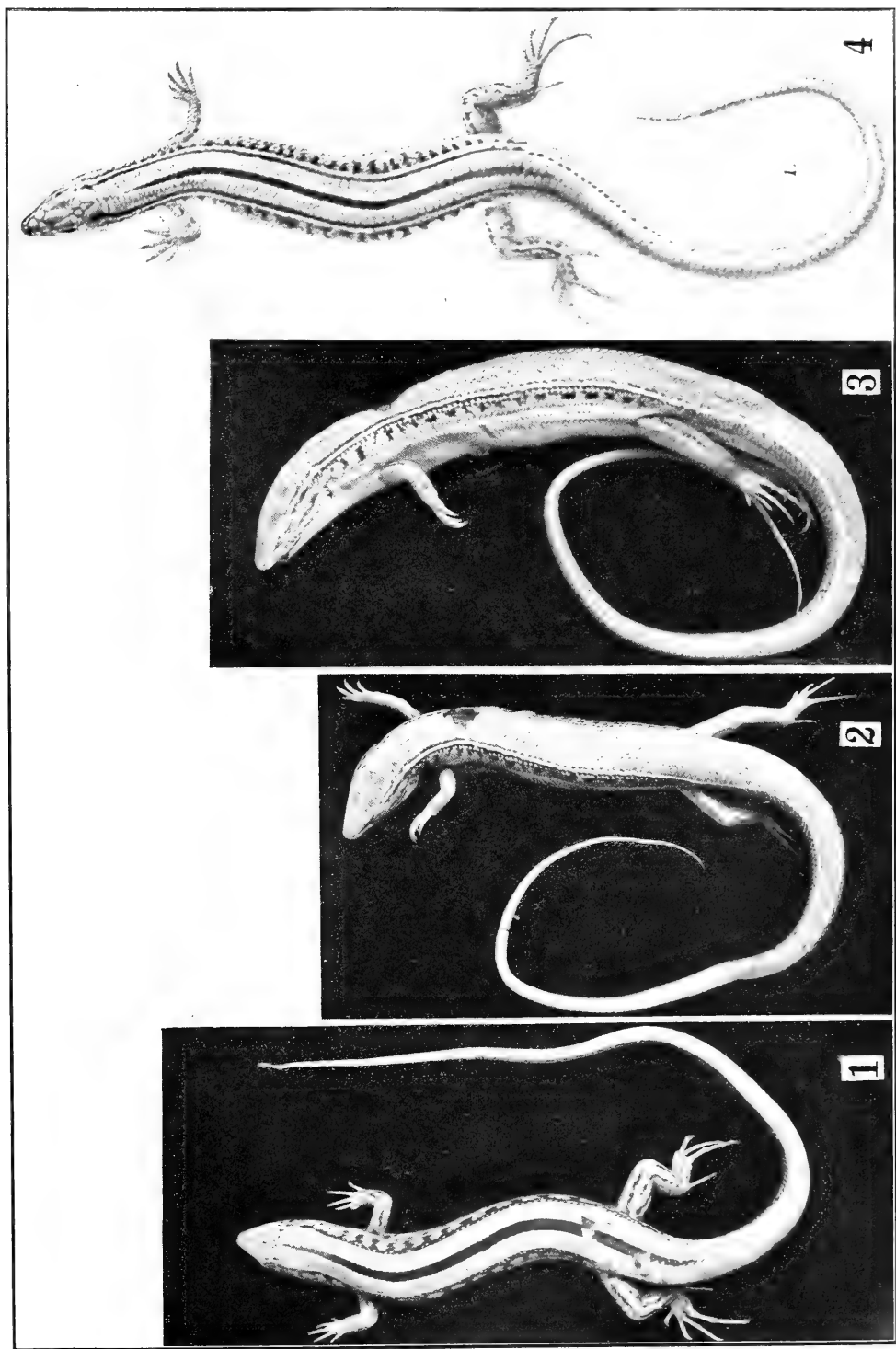






Properties of Certain Fungicidal Compounds.





Reptiles in the Macleay Museum.



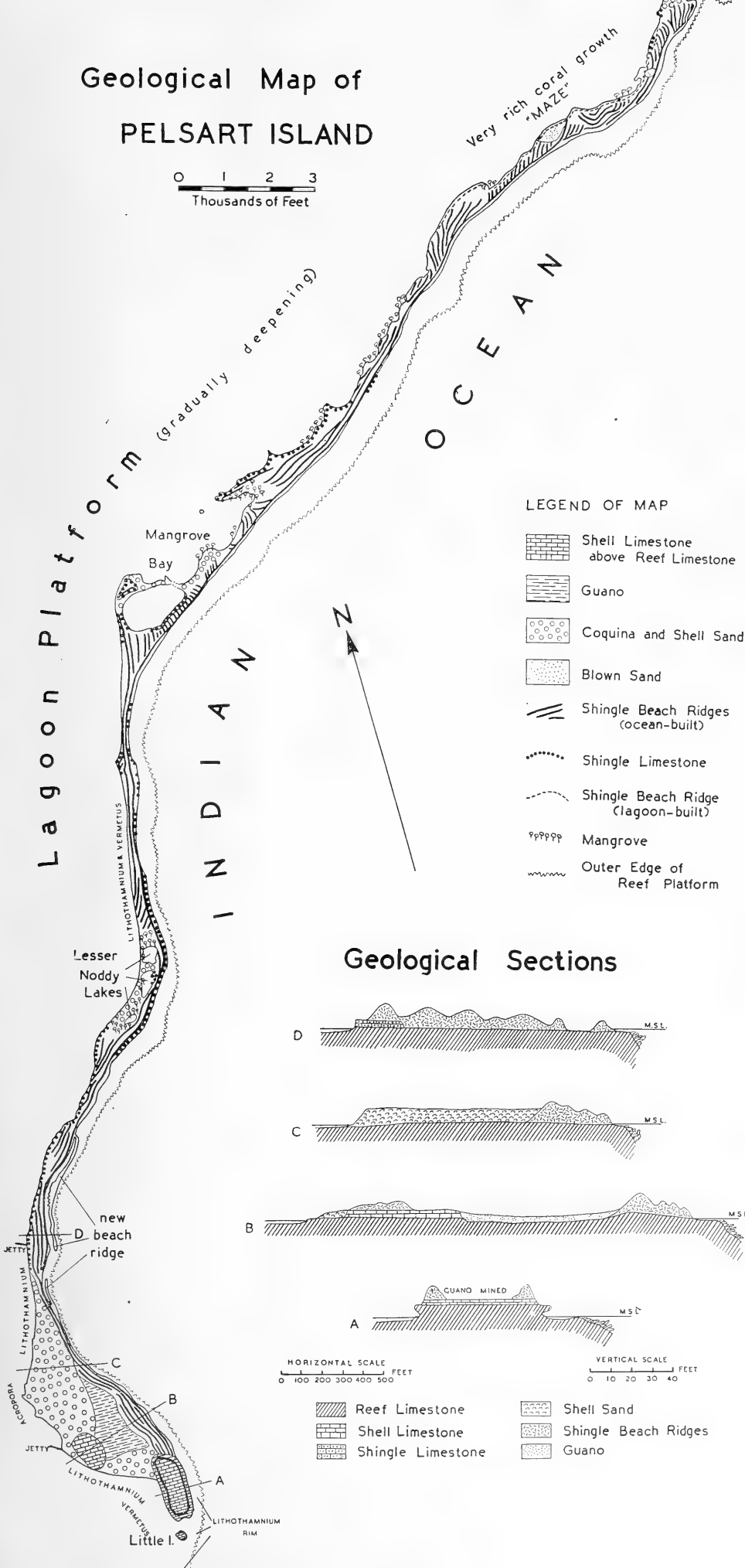
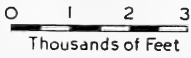


Rhythmic Banding in Ordovician Strata.





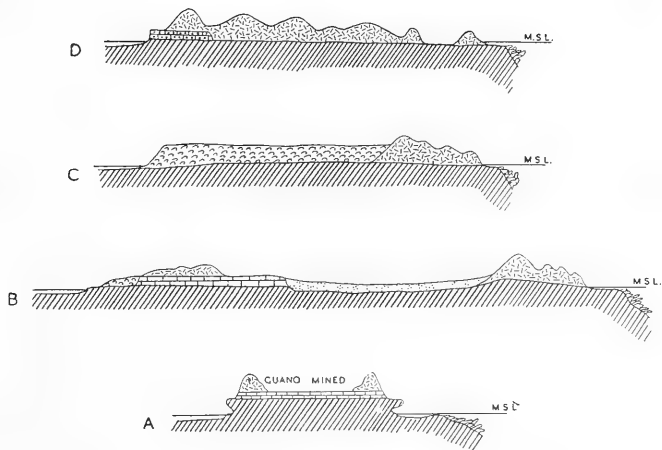
# Geological Map of PELSART ISLAND



## LEGEND OF MAP

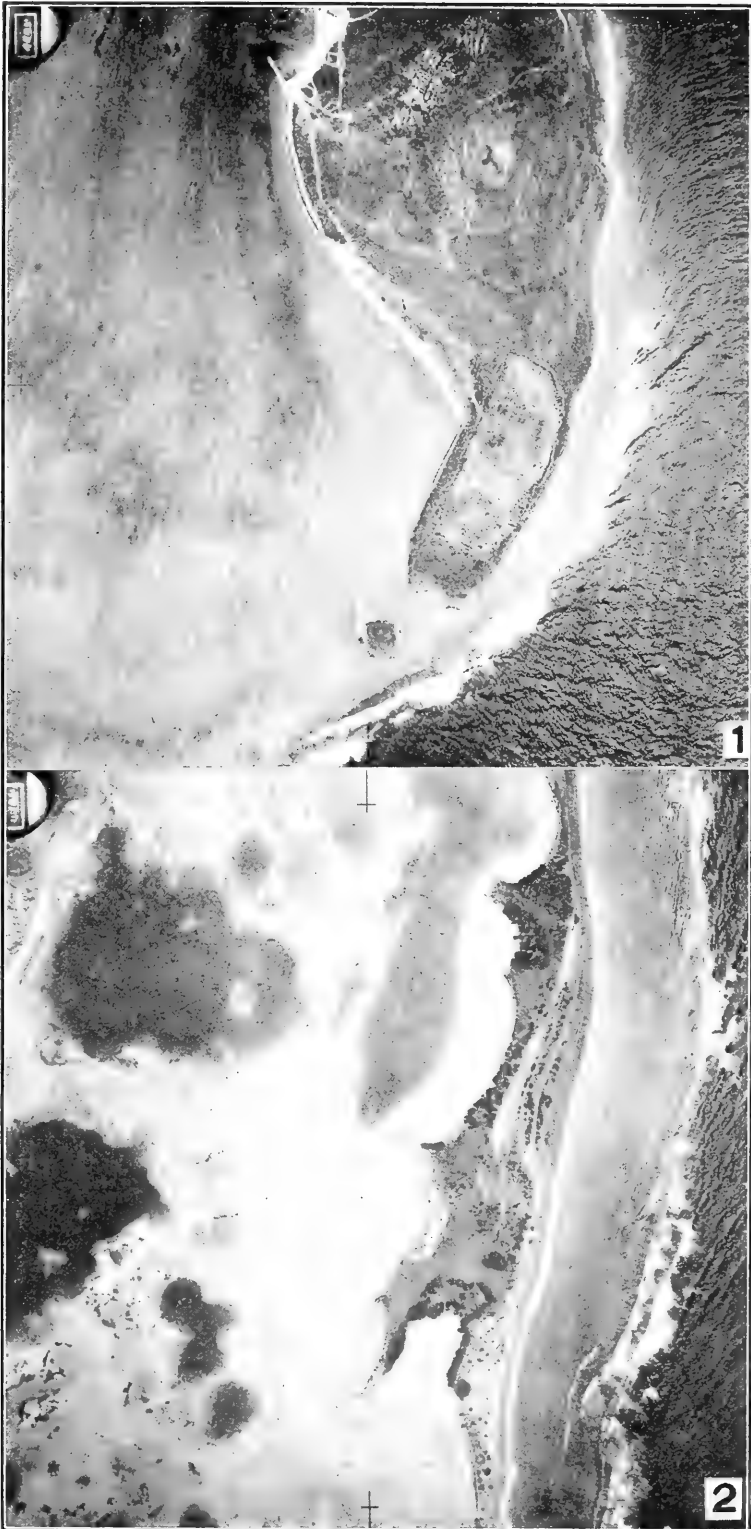
- Shell Limestone above Reef Limestone
- Guano
- Coquina and Shell Sand
- Blown Sand
- Shingle Beach Ridges (ocean-built)
- Shingle Limestone
- Shingle Beach Ridge (lagoon-built)
- Mangrove
- Outer Edge of Reef Platform

## Geological Sections



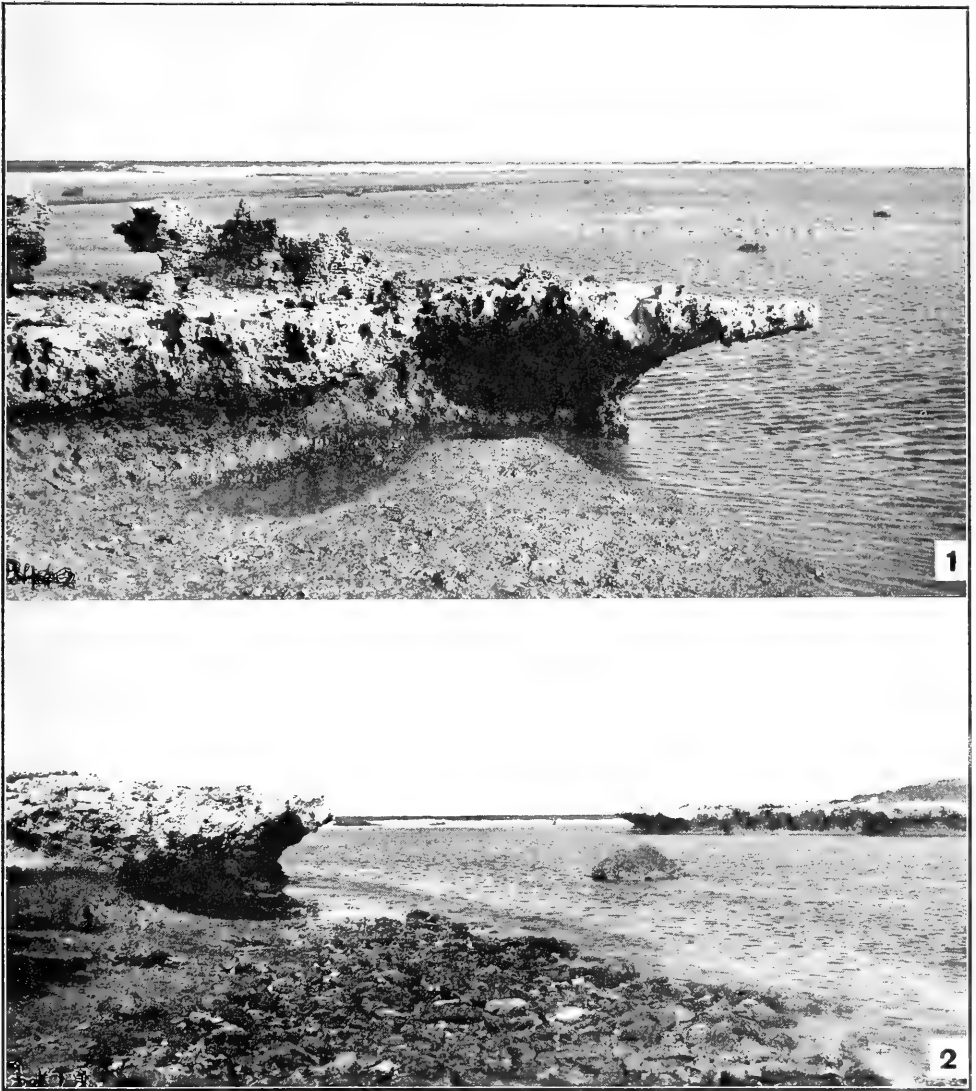
- Reef Limestone
- Shell Limestone
- Shingle Limestone
- Shell Sand
- Shingle Beach Ridges
- Guano





Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.







Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.

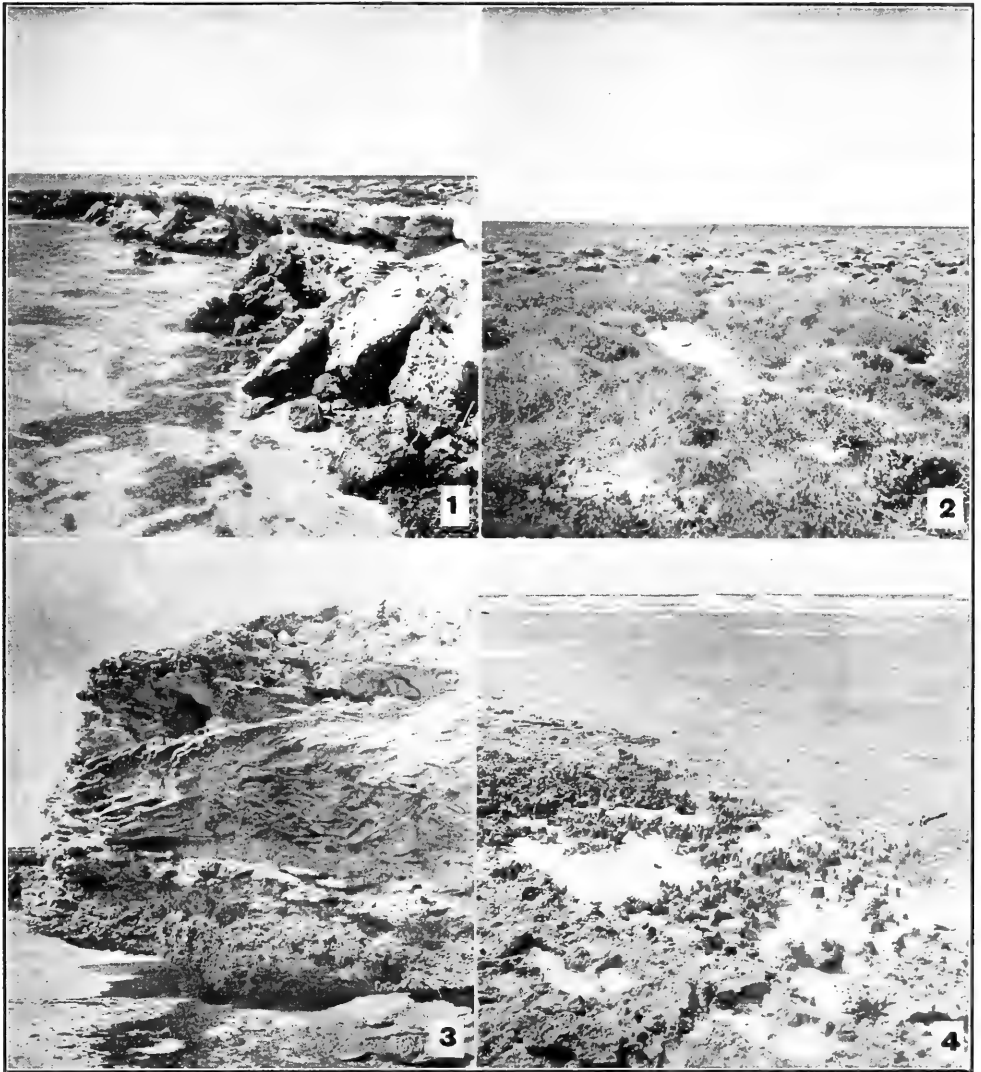




Geology of Houtman's Abrolhos, Western Australia.







Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.





Geology of Houtman's Abrolhos, Western Australia.



## DISTRIBUTION OF MICROSPORE TYPES IN NEW SOUTH WALES PERMIAN COALFIELDS.

By J. A. DULHUNTY, D.Sc., Commonwealth Research Fellow in Geology,  
University of Sydney.

(Five Text-figures.)

[Read 25th September, 1946.]

### INTRODUCTION.

In a recent publication (Dulhunty, 1945), the author described the principal microspore-types found in New South Wales Permian coal seams. A tabular system of type-numbering was suggested, and spore types were illustrated by photomicrographs and line-drawings. For details of different types referred to in the present paper, and the method of type-numbering used, reference should be made to the above publication. For the convenience of readers, however, an abridged key to the spore-types is given in Table 1.

TABLE 1.  
*Abridged Key to Spore-Types.*

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Examples of type-numbering: P2A, P29B, P34C, P40D.

Letter P preceding type-number indicates Permian type.

Letter A, B, C or D following type-number indicates variations in size or minor details of spores belonging to the same general type.

Type-numbers (2, 29, 34, 40 in above examples) refer to body-shape, tetrad scar and ornamentation, as follows:

<p>1 Angular tetrahedral; trilete; psilate. 2 Sub-ang. tetrahedral; trilete; psilate. 3 Ellipsoidal; monolete; psilate. 4 Spheroidal; trilete; psilate. 5 Spheroidal; monolete; psilate. 6 Ang. tetrahedral; trilete; granulate. 7 Sub-ang. tetrahedral; trilete; granulate. 8 Ellipsoidal; monolete; granulate. 9 Spheroidal; trilete; granulate. 10 Spheroidal; monolete; granulate. 13 Ellipsoidal; monolete; reticulate. 14 Spheroidal; trilete; reticulate. 15 Spheroidal; monolete; reticulate. 16 Ang. tetrahedral; trilete; echinate. 17 Sub-ang. tetrahedral; trilete; echinate.</p>	<p>18 Ellipsoidal; monolete; echinate. 19 Spheroidal; trilete; echinate. 20 Spheroidal; monolete; echinate. 21 Ang. tetrahedral; trilete; striate. 23 Ellipsoidal; monolete; striate. 26 Ang. tetrahedral; trilete; verrucate. 28 Ellipsoidal; monolete; verrucate. 29 Spheroidal; trilete; verrucate. 30 Spheroidal; monolete; verrucate. 32 Sub-ang. tetrahedral; trilete; monowinged. 33 Ellipsoidal; monolete; monowinged. 34 Spheroidal; trilete; monowinged. 35 Spheroidal; monolete; monowinged. 38 Ellipsoidal; monolete; biwinged. 40 Spheroidal; monolete; biwinged.</p>
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This paper deals with stratigraphical distribution of microspores in different coal measures, and palaeogeographical distribution in the principal coalfields, as well as variations in relative abundance and diversity of types. Distribution is first considered from the viewpoint of individual types, and then in terms of groups of morphologically-related types and groups of types possessing similar forms of ornamentation. No attempt is made to discuss continuity of assemblages on specific coal-bearing horizons or stratigraphical variation between individual seams, as insufficient data are at present available.

The work was carried out as a preliminary survey of different aspects of microspore distribution, with the object of revealing promising fields in which subsequent research may provide results of value in palaeobotany or stratigraphy.

MATERIAL EXAMINED.

Spore-counts were carried out in concentrates prepared from a series of forty-seven representative samples taken from coal seams in different coal measures and coalfields of the main Permian basin in central eastern New South Wales. The geographical distribution of samples selected for examination, and the arbitrary subdivision of the Permian coal-province into coalfields adopted for the present purpose, are illustrated in Fig. 1.

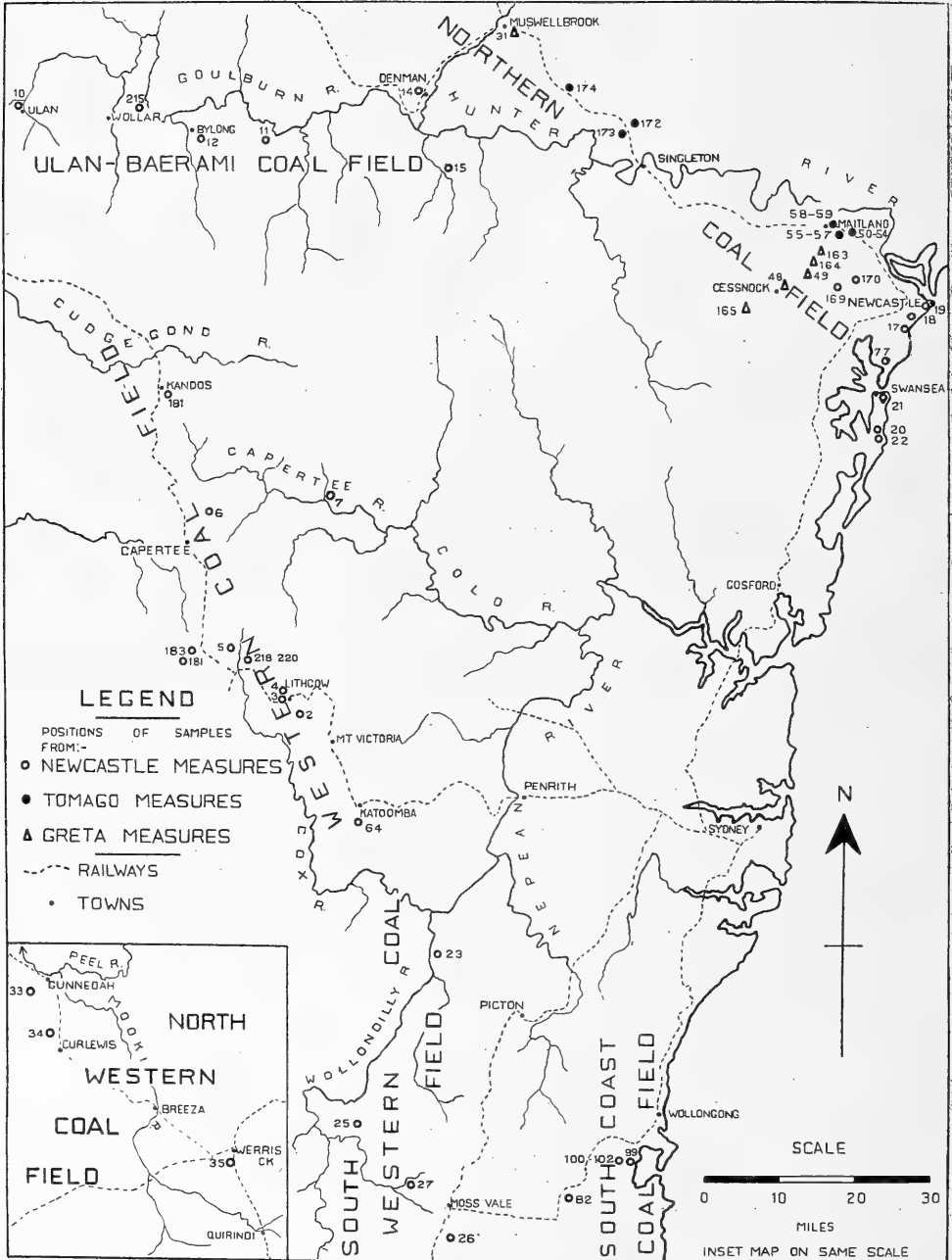


Fig. 1.—Central eastern New South Wales, showing Permian Coalfields and positions of coal samples.



The stratigraphical subdivision of Permian strata into coal measures (David, 1932; Raggatt, 1938; Jones, 1939) is shown in Table 2.

TABLE 2.  
*Stratigraphical Subdivision of Permian Strata in New South Wales.*

PERMIAN.	Upper Coal Measures.	Newcastle Stage.
		Tomago Stage.
	Upper Marine.	
	Lower or Greta Coal Measures.	
	Lower Marine.	

The Tomago and Newcastle Stages of the Upper Coal Measures are referred to, for convenience, as the Tomago and Newcastle Measures, it being understood that they are actually stages of the one coal-measure series.

Details regarding samples collected for spore-counts are given in Table 3 which shows the number of samples collected from each seam, and the stratigraphical sequence of seams in the different coalfields and measures.

Material was collected from as many seams as possible in the principal area of Permian coal-measure deposition. Samples from outlying areas, where correlation with measures in the main basin was uncertain, or where conditions of sedimentation may have been specialized, were not included, as the objects of the work were to determine stratigraphical ranges of microspore-types in measures of known sequence, and to study general distribution resulting from normal variation of conditions from central to marginal environments of deposition in the main coal basin. It is hoped to deal with outlying areas, and examine the possibility of their correlation with the main basin, in a subsequent publication.

Well-preserved microspores were found to occur abundantly in all coal seams except those in the South Coast Coalfield, where it was difficult to obtain seam-samples with sufficient spores for satisfactory spore-counts. Concentrates were prepared from over twenty samples collected from all seams there, but only three of them had sufficient spores for reliable counts. These, as indicated in Table 2, were from No. 3 and No. 4 seams. This leaves the other five seams unrepresented, so that assemblages of types and groups for the South Coast Coalfield, illustrated in this paper, may not represent a true average for all seams.

In the majority of samples from this Coalfield, unidentifiable remains of spores are present as almost opaque material which will not take safranin stain; and fragments of translucent plant-tissue, showing cell structure, are rare and will not stain. In view of this and also that the coal is known to contain more carbon and yield more fixed carbon than other New South Wales coals, it is probable that rarity of identifiable spores is due to advanced metamorphism rather than absence of spores in the original coal-forming débris.

#### TREATMENT OF MATERIAL AND METHOD OF MAKING SPORE-COUNTS.

Coal samples representing full sections of seams were taken where outcrop material was sufficiently fresh, otherwise the full height of working faces was sampled in mines. Each sample was crushed, mixed and reduced to about 5 lb. weight of coal passing a sieve of  $\frac{1}{16}$ " mesh.

Spore concentrates, prepared by oxidation and solution of the coal, were mounted for microscopical examination by the method already described (Dulhunty, 1945). Three mounts of each concentrate were examined, under a magnification of 200 diameters, by working across the slides in different directions, and counting spore-types to a total number of several hundred. The number belonging to each individual type was then

expressed as a percentage of the total identified in each concentrate, and results were used for statistical studies.

TABLE 3.  
*Particulars of Samples used for Spore-Counts.*

Serial Nos. of Samples.	Seam.	Coalfield.	Coal Measures.
7, 64, 4 .. ..	Katoomba.	Western.	Newcastle Stage, Upper Coal Measures.
6 .. .. .	Dirty.	"	" " " " "
183, (218-220).. ..	Irondale.	"	" " " " "
2, 3, 5, 181 .. ..	Lithgow.	"	" " " " "
15, 14, 22 .. ..	Wallarah or Top.	Northern.	" " " " "
20 .. .. .	Great Northern.	"	" " " " "
77 .. .. .	Fassifern.	"	" " " " "
21 .. .. .	Pilot.	"	" " " " "
17 .. .. .	Burwood.	"	" " " " "
18 .. .. .	Nobby's.	"	" " " " "
19 .. .. .	Dirty.	"	" " " " "
170 .. .. .	Young Wallsend.	"	" " " " "
169 .. .. .	Borehole.	"	" " " " "
34, 35, 33 .. ..	Seams at Gunnedah, Curlewis, Werris Creek.	North-western.	" " " " "
11 .. .. .	Top. (? Katoomba Horiz.)	Ulan-Baerami.	" " " " "
12, 215 .. .. .	Seam below Top. (? Dirty Horizon.)	" "	" " " " "
10 .. .. .	Bottom. (? Lithgow Horizon.)	" "	" " " " "
99 .. .. .	No. 3 or Dirty.	South Coast.	" " " " "
82, (100-102) .. ..	No. 4.	" "	" " " " "
23 .. .. .	No. 1 or Bulli.	South-western.	" " " " "
25, 26, 27 .. ..	No. 3 or Dirty.	" "	" " " " "
(58-59) .. .. .	Big Ben or Tomago Thick.	Northern.	Tomago Stage, Upper Coal Measures.
(50-54), (55-57) .. ..	Rathluba.	"	" " " " "
174 .. .. .	Liddell.	"	" " " " "
172, 173 .. .. .	Rix Creek.	"	" " " " "
31, 48, 49, 164, 165, 163	Greta.	"	Greta Coal Measures.

#### VARIATION IN DIVERSITY OF SPORE-TYPES.

This was investigated by expressing the number of different types identified in each sample as a percentage of the forty-eight types found in New South Wales Permian

coals, and the average percentages of types present in coals from different measures and coalfields were then obtained. Average results (Table 4) are shown for Greta and Tomago Measures in the Northern Coalfield, and for the Newcastle Measures in all coalfields, as well as separate coalfields.

TABLE 4.  
*Table showing Diversity of Spore-Types in Different Measures and Coalfields.*

Newcastle Measures (all coalfields)	..	..	..	..	62.0%
Tomago Measures (Northern Coalfield)	..	..	..	..	68.5%
Greta Measures (Northern Coalfield)	..	..	..	..	62.8%
Newcastle Measures :					
South Coast Coalfield	..	..	..	..	46.5%
South-western Coalfield	..	..	..	..	67.8%
Western Coalfield	..	..	..	..	64.8%
Ulan-Baerami Coalfield	..	..	..	..	66.7%
Northern Coalfield	..	..	..	..	67.3%
North-western Coalfield	..	..	..	..	59.1%

There is relatively little variation in the average percentages. Coals from Tomago Measures show a greater variety of types than those from Greta Measures or Newcastle Measures in all coalfields. Figures for Newcastle Measures in separate coalfields are reasonably constant, except for the South Coast Coalfield, where they are low. This may be due to the limited number of samples examined, or to destruction of some spore-types by metamorphism.

In general, no variation of special significance is revealed in diversity of types present in the different coals.

RELATIVE ABUNDANCE OF SPORE-TYPES.

The average relative abundance of individual spore-types in coals from all measures and fields was determined by obtaining the average percentage for each type. The results were then illustrated graphically by arranging the spore-types in order of abundance from left to right, with vertical columns above the types proportional to their average percentages. The diagram obtained is shown in Fig. 2. It indicates that

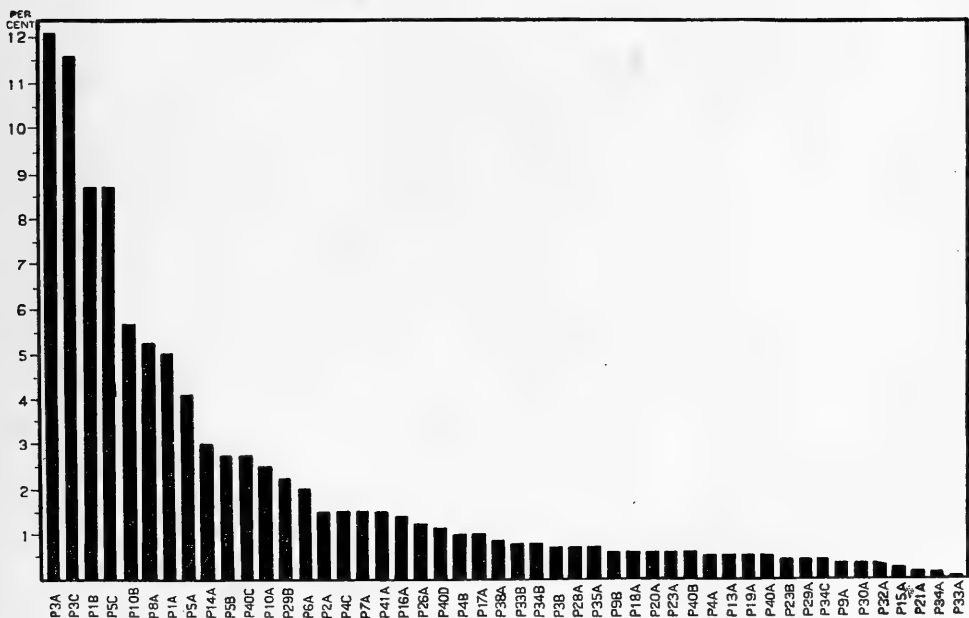


Fig. 2.—Relative abundance of microspore-types.

a small number of types predominates in abundance, and that the majority occur far less frequently.

The four most abundant spores are psilate: the ellipsoidal-monolete types P3A and P3C, amounting to 12.1 and 11.6 per cent. respectively, and the tetrahedral-trilete type P1B and the spheroidal-monolete type P5C each representing 8.7 per cent. These are followed by the two granulate types P10B and P8A, between 5 and 6 per cent.: both are monolete and differ only in their spheroidal and ellipsoidal shapes, respectively. Next come the small psilate types P1A, trilete, and P5A, monolete, between 4 and 5 per cent. The most abundant spore-types are all simple forms, and include the smallest of the Permian types recorded. Of the remaining forty types, six have averages between 2 and 3 per cent., nine between 1 and 2 per cent., and twenty-five less than 1 per cent.

#### PALAEOGEOGRAPHICAL DISTRIBUTION OF SPORE-TYPES IN THE NEWCASTLE MEASURES.

Study of palaeogeographical distribution was confined to variations in average relative abundance, and presence or absence of spore-types in the Newcastle Measures throughout the different coalfields. Greta and Tomago measures were not included, as typical outcrops occur only in the Northern Coalfield, and insufficient data are yet available for the study of palaeogeographical variations within that coalfield.

In each spore-count on coals from the Newcastle Measures, numbers of spores belonging to different types were expressed as percentages of the total number identified. The average percentage for each type was then obtained in all samples from each of the coalfields. Results for average relative abundance of each type thus obtained are given in Table 5 under the heading "Palaeogeographical Distribution". The absence of a spore-type in all samples from any particular coalfield is indicated by the letter A.

Table 5 shows considerable variation in relative abundance of spore-types throughout the different coalfields. This is most marked in the less common types, P16A, P18A, P33B and P40D, which are from four to six times more numerous in some fields than others. The more common types, P3C, P3A, P1A and P8A, show much less variation.

In some cases there is evidence of progressive variation in relative abundance either from north to south or from marginal to central facies of coal-measure deposition. In the Newcastle Measures, types P1B and P33B are most numerous in southern districts, become less abundant in the Ulan-Baerami and Northern Coalfields, and reach a minimum in the North-Western field. P40C is more abundant in North-Western and Northern coalfields than in the South Coast and South-Western fields. P2A and P40A reach maximum development in the Northern Coalfield—particularly between Newcastle and Swansea, where conditions of deposition were approximately central—and become less numerous in areas of marginal deposition. Type P3C is most abundant in marginal facies within the Ulan-Baerami, Western and South-Western Coalfields, is less numerous in the North-Western and South Coast fields, and reaches a minimum in the Northern Coalfield, where central conditions prevailed. Other types are more abundant in different fields which do not appear to be geographically related. Type P1A, for example, reaches 9.2 and 10.3 per cent. in the Northern and South-Western Coalfields, respectively, while in other areas it varies from 3 to 6 per cent.

Table 5 shows also several instances in the Newcastle Measures where spore-types are present in some coalfields and absent in others. This occurs with rarer types, and, in some cases, there is a possible relationship between absence of spores and palaeogeography. For example, five spore-types (P19A, P21A, P33A, P35A, P40A) are present in all areas except the South-Coast and North-Western Coalfields, which represent the southern and northern extremities of coal-measure deposition in the area at present under consideration. In another case, type P34C is present in all marginal areas of deposition, but absent where central conditions obtained in the Northern Coalfield.

#### STRATIGRAPHICAL DISTRIBUTION OF SPORE-TYPES.

Stratigraphical distribution of spore-types in Greta, Tomago and Newcastle Measures was studied by obtaining average relative percentages for types in all samples from each of the three measures. Results are given in Table 5 under the heading "Strati-

graphical Distribution". Of the forty-eight different types, thirty-four occur in all measures, and the remaining fourteen types appear to have limited ranges.

Ranges and relative abundance of the fourteen limited types, together with examples of variation in abundance of types common to all measures, are illustrated in Fig. 3. Of the three rectangles opposite each spore-type in this diagram, the one completely filled-in represents the coal measures in which maximum development occurs. The other

TABLE 5.  
*Stratigraphical and Palaeogeographical Distribution of Microspores.*

Spore-Types.	Stratigraphical Distribution.			Palaeogeographical Distribution.					
	Newcastle Measures. All Coalfields.	Tomago Measures. All Coalfields.	Greta Measures. All Coalfields.	Newcastle Measures: Different Coalfields.					
				Northern.	South Coast.	South-Western.	Western.	Ulan-Baerami.	North-Western.
P1A ..	6.4	6.3	2.4	9.2	5.7	10.3	4.2	3.1	6.0
P1B ..	6.0	8.3	11.9	5.8	10.6	6.4	5.8	4.0	3.5
P2A ..	2.2	1.6	0.7	4.5	1.6	1.4	1.6	3.3	0.9
P3A ..	11.3	11.5	13.8	11.1	13.3	12.7	9.0	11.4	10.7
P3B ..	1.1	0.9	A	1.0	0.8	1.2	1.4	1.1	1.4
P3C ..	13.8	8.5	12.5	8.5	13.0	14.9	15.1	17.3	14.0
P4A ..	0.5	0.6	0.5	0.8	0.1	0.3	0.4	1.2	0.3
P4B ..	0.9	0.6	1.7	0.6	1.8	0.2	1.5	0.6	0.6
P4C ..	1.3	1.5	1.6	1.2	0.6	1.6	1.3	1.3	1.7
P5A ..	5.5	3.1	3.6	3.7	5.7	7.8	5.6	5.4	5.2
P5B ..	3.2	2.3	2.7	2.9	4.3	4.5	2.8	2.4	2.3
P5C ..	10.1	6.5	9.5	4.3	10.4	9.5	10.9	10.7	14.9
P6A ..	1.1	1.9	3.0	1.2	A	1.1	1.0	1.4	1.7
P7A ..	1.1	2.3	1.2	1.0	0.8	0.4	1.2	1.9	1.1
P8A ..	5.6	6.1	4.2	7.3	3.4	2.9	6.8	6.4	6.7
P9A ..	0.2	0.6	A	0.3	A	A	0.5	0.3	A
P9B ..	0.9	0.2	0.6	0.5	0.4	0.1	2.1	2.1	0.3
P10A ..	2.3	2.6	2.7	3.2	1.0	2.1	3.1	2.2	2.4
P10B ..	5.3	7.1	4.7	6.8	5.6	3.4	5.7	3.2	6.9
P13A ..	0.6	1.0	A	1.0	0.4	0.7	0.5	1.1	A
P14A ..	3.6	2.5	2.8	1.8	6.5	2.1	4.5	2.9	3.7
P15A ..	A	A	0.7	A	A	A	A	A	A
P16A ..	1.1	2.9	0.1	1.0	0.6	1.3	0.8	1.1	2.0
P17A ..	1.1	2.0	0.3	1.2	1.0	1.8	0.6	0.8	1.4
P18A ..	0.6	0.8	0.3	0.6	1.4	0.3	0.2	A	1.1
P19A ..	0.3	1.0	0.1	0.8	A	0.3	0.1	0.5	A
P20A ..	0.5	1.2	0.1	0.3	0.6	0.6	0.4	0.4	0.6
P21A ..	0.3	A	A	0.2	A	0.7	0.2	0.6	A
P23A ..	0.5	0.5	0.9	0.9	0.4	0.3	0.4	0.3	0.3
P23B ..	0.4	0.4	0.3	0.4	0.8	0.9	0.1	A	0.3
P26A ..	0.4	0.6	3.0	0.8	A	0.6	A	0.6	0.7
P28A ..	0.1	A	1.9	0.3	A	0.1	A	A	A
P29A ..	0.1	A	1.2	0.4	A	0.3	A	0.1	A
P29B ..	1.3	0.1	5.2	1.5	1.8	1.7	1.5	1.0	A
P30A ..	A	0.3	0.5	A	A	A	A	A	A
P32A ..	A	A	1.0	A	A	A	A	A	A
P33A ..	0.1	A	A	0.2	A	0.1	0.1	0.4	A
P33B ..	0.5	1.8	A	0.4	1.2	0.5	0.6	0.3	A
P34A ..	0.3	A	A	A	A	0.8	0.2	0.1	0.7
P34B ..	0.8	0.7	0.8	0.1	0.8	1.1	1.2	0.6	1.1
P34C ..	0.4	0.7	0.2	A	0.3	1.0	0.3	0.3	0.6
P35A ..	0.2	1.4	0.4	0.3	A	0.3	0.4	0.1	A
P38A ..	0.7	1.7	0.2	0.8	1.0	0.8	0.9	0.5	0.4
P40A ..	0.8	0.7	A	2.5	A	0.9	0.5	0.6	A
P40B ..	1.3	0.4	A	1.6	1.6	0.7	1.5	1.1	1.1
P40C ..	3.1	3.7	1.0	5.6	1.3	2.8	2.0	2.7	4.1
P40D ..	0.8	2.4	0.5	1.8	0.1	0.3	1.1	1.0	0.7
P41A ..	1.2	1.1	2.3	1.9	0.7	0.5	1.8	1.5	1.1

two are filled-in according to the fractions of the maximum abundance their spore-percentages represent. For example, the Greta-Measures rectangle for P1B is completely filled-in, having a maximum abundance of 11.9%. The Newcastle-Measures rectangle for P2A is entirely filled-in, having a maximum abundance of 2.2%. In each case the remaining two rectangles are filled-in to fractions of 11.9% and 2.2% respectively. Where a spore-type is absent, the base of the rectangle is shown by a broken line.

SPORE TYPE	GRETA MEASURES	UPPER COAL MEASURES	
		TOMAGO STAGE	NEWCASTLE STAGE
P1B	██████████	██████████	██████████
P2A	██████████	██████████	██████████
P3C	██████████	██████████	██████████
P10B	██████████	██████████	██████████
P28A	██████████	-----	██████████
P29A	██████████	-----	██████████
P21A	-----	██████████	██████████
P33A	-----	██████████	██████████
P34A	-----	██████████	██████████
P40B	-----	██████████	██████████
P40A	-----	██████████	██████████
P33B	-----	██████████	██████████
P13A	-----	██████████	██████████
P3B	-----	██████████	██████████
P9A	-----	██████████	██████████
P30A	██████████	██████████	-----
P32A	██████████	-----	██████████
P15A	██████████	-----	-----

Fig. 3.—Stratigraphical distribution of certain microspore-types.

Four examples of variation in abundance of types common to all measures are illustrated at the top of the diagram. Type P1B has maximum development in Greta Measures, and minimum in the Newcastle Measures. On the other hand, P2A shows progressive increase in abundance from Greta to Newcastle Measures. Irregular trends are shown by other types such as P3C, which is more abundant in Greta and Newcastle Measures, and P10B, which reaches maximum development in Tomago coals.

Of the fourteen types with limited ranges, P32A and P15A have been found only in Greta Measures, and P30A has been identified in Greta and Tomago Seams, but not in the Newcastle Measures. Six types, P40B, P40A, P33B, P13A, P3B and P9A, occur in Tomago and Newcastle Measures, but have not been found in Greta-Measures. Three of these reach maximum development in the Newcastle Measures, and the other three in Tomago Measures. Three spore-types, P21A, P33A and P34A, have been recognized only in Newcastle Measures. Types P28A and P29A have been found in Greta and Newcastle coals, but not in Tomago coals.

The foregoing results must be confirmed or modified by subsequent work on large numbers of samples, but Fig. 3 suggests that certain types have limited ranges and it is possible that they may eventually be used as determinative fossils in correlating Permian strata. Caution is necessary, however, particularly in correlating widely separated occurrences which may have accumulated under different conditions of deposition, as a type may be absent from the marginal facies of a series and yet be present in central regions. Evidence of restricted palaeogeographical distribution of this nature was found in the Newcastle Measures, as already discussed.

#### GROUPS OF MICROSPORE-TYPES.

This section deals with relative abundance and distribution of microspores in terms of groups. The work was carried out as characteristic assemblages of groups may prove useful in stratigraphical correlation or the study of Permian floral assemblages.

Spore-types were divided into two series of seven groups: those which appeared to be morphologically related, and those which possessed similar forms of ornamentation. The first series (A to G), referred to as "Morphological Groups", bring together spores with similar fundamental features, such as nature of tetrad scar or dehiscence, body-shape and number of wings, irrespective of ornamentation. In the second series (1 to 7), referred to as "Ornamentation Groups", the spores are grouped on the basis of general forms of ornamentation and presence of wings, without respect to body-shape or dehiscence. The essential features of the seven groups in each series, and the spore-types allotted to each group, are shown in Table 6.

TABLE 6.  
*Grouping of Microspores.*

Groups.	Character of Group.	Permian Spore-Types. (See Table 1.)	
Morphological.	A	Tetrahedral; Trilete.	P—1A, 1B, 2A, 6A, 7A, 16A, 17A, 21A, 26A.
	B	Spheroidal; Trilete.	P—4A, 4B, 4C, 9A, 9B, 14A, 19A, 29A, 29B, 41A.
	C	Monowinged; Trilete.	P—32A, 34A, 34B, 34C.
	D	Spheroidal; Monolete.	P—5A, 5B, 5C, 10A, 10B, 15A, 20A, 30A.
	E	Ellipsoidal; Monolete.	P—3A, 3B, 3C, 8A, 13A, 18A, 23A, 23B, 28A.
	F	Monowinged; Monolete.	P—33A, 33B, 35A.
	G	Biwinged; Monolete.	P—38A, 40A, 40B, 40C, 40D.
Ornamentation.	1	Psilate.	P—1A, 1B, 2A, 3A, 3B, 3C, 4A, 4B, 4C, 5A, 5B, 5C, 41A.
	2	Granulate.	P—6A, 7A, 8A, 9A, 9B, 10A, 10B.
	3	Reticulate.	P—13A, 14A, 15A.
	4	Echinate.	P—16A, 17A, 18A, 19A, 20A.
	5	Striate.	P—21A, 23A, 23B.
	6	Verrucate.	P—26A, 28A, 29A, 29B, 30A.
	7	Winged.	P—32A, 33A, 33B, 34A, 34B, 34C, 35A, 38A, 40A, 40B, 40C, 40D.

Variations in abundance and distribution were investigated by obtaining averages for abundance of types belonging to different groups. In each spore-count the number of spores belonging to each group was expressed as a percentage of the total number

identified. Averages were then obtained for the different groups in all samples from each of the coal measures and coalfields. Finally, averages were calculated for each group in the whole of the Permian. Results are given in Table 7.

TABLE 7.  
*Stratigraphical and Palaeogeographical Distribution of Microspore-Groups.*

Spore-Groups.		Whole of Permian.	Stratigraphical Distribution.			Palaeogeographical Distribution.					
			New-castle Measures All Coal-fields.	Tomago Measures Northern Coal-field.	Greta Measures Northern Coal-field.	Newcastle Measures: Separate Coalfields.					
						South Coast.	South-Western.	Western.	Ulan-Baerami.	Northern.	North Western.
Morphological.	A	22.5	19.6	25.5	22.5	20.2	23.3	15.5	16.7	24.9	17.1
	B	11.5	10.3	8.1	16.0	12.3	7.1	13.6	11.1	9.8	7.8
	C	1.6	1.4	1.4	2.0	1.1	2.2	1.7	0.9	A	2.4
	D	24.9	27.4	23.0	24.4	27.7	27.9	28.5	26.7	21.2	32.4
	E	32.5	34.1	29.6	33.7	33.6	34.0	33.4	38.0	31.1	34.4
	F	1.5	0.8	3.2	0.4	1.2	1.0	1.1	0.8	0.9	A
	G	5.8	6.7	9.1	1.7	4.0	5.6	6.0	5.9	12.4	6.3
Ornamentation.	1	60.0	64.2	52.7	63.0	69.0	71.2	61.2	65.6	55.4	62.5
	2	17.8	16.5	20.5	16.3	11.2	10.0	20.4	17.9	20.3	19.1
	3	3.7	4.2	3.5	3.5	6.9	2.8	5.0	4.0	2.8	3.7
	4	4.1	3.6	7.8	0.8	3.6	3.7	2.2	2.6	4.5	5.1
	5	1.0	1.2	0.8	1.1	1.3	1.9	0.8	0.8	1.5	0.7
	6	4.9	1.9	1.0	11.8	1.6	2.7	1.5	1.7	3.0	0.7
	7	9.5	8.9	13.7	6.0	6.4	8.6	8.8	7.6	13.4	8.6

#### RELATIVE ABUNDANCE OF MICROSPORES BELONGING TO DIFFERENT GROUPS.

Relative abundance of spores in the seven groups of each series in all coalfields and measures is illustrated in Fig. 4. Morphological and Ornamentation Groups are arranged in order of abundance from left to right. Vertical columns above group letters and numbers indicate relative average percentages for all types in each group.

The Morphological Groups show comparatively even gradation in relative abundance. Group E (ellipsoidal-monolete) representing 32.5 per cent. is followed by Group D (spheroidal-monolete), 24.9 per cent.; Group A (tetrahedral-trilete), 22.5 per cent.; and Group B (spheroidal-trilete), 11.5 per cent. The three remaining groups, including winged spores, have averages of less than 10 per cent. Of these, Group G (biwinged-monolete) is most common, while Group C (monowinged-trilete) and Group F (monowinged-monolete) are comparatively rare. In general, monolete spores are more numerous than trilete in both winged and non-winged groups.

The Ornamentation Groups show a decidedly uneven gradation in relative abundance. Psilate spores, Group 1, averaging 60 per cent., are three times more numerous than granulate types, Group 2, averaging 17.8 per cent. Winged spores, Group 7, are next with 9.5 per cent. These are followed by the verrucate, echinate and reticulate types, Groups 6, 4 and 3, respectively, averaging between 3 and 5 per cent. The least common are the striated spores, Group 5, averaging 1 per cent.



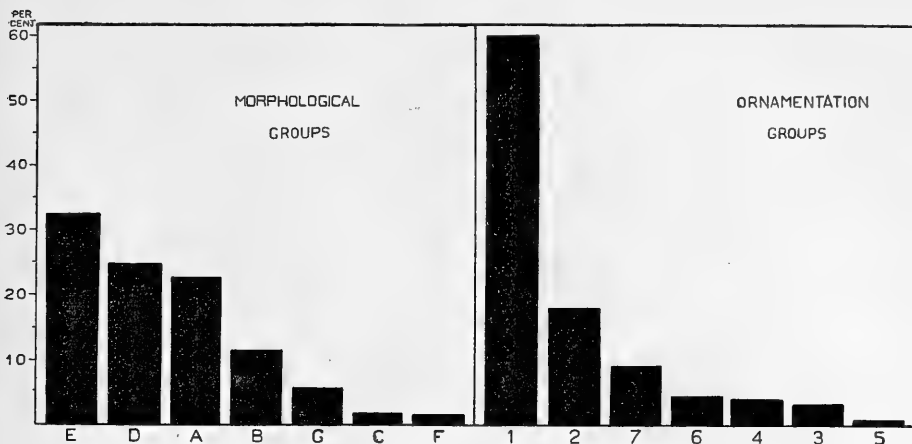


Fig. 4.—Relative abundance of microspores belonging to different groups.

#### STRATIGRAPHICAL DISTRIBUTION OF MICROSPORE-GROUPS.

Figures for average percentages given in Table 7 show variation in abundance for both series of groups throughout Greta, Tomago and Newcastle Measures. The results are illustrated graphically in Fig. 5. Vertical columns, proportional to percentages for each group, stand opposite different coal measures. The diagram illustrates stratigraphical variation for each group, and also assemblages for both series of groups in the three different coal measures.

The majority of Morphological Groups show very little stratigraphical variation, particularly the more abundant Groups, E, D and A. Of the less abundant groups, G and F attain maximum development in Tomago Measures, while Group C is most numerous in Newcastle Measures. The Ornamentation Groups show greater stratigraphical variation. The abundant psilate spores, Group 1, are more numerous in Greta and Newcastle Measures than in the Tomago. Echiniate spores, Group 4, show a well-defined maximum in Tomago Measures. Verrucate types, Group 6, are more than five times as numerous in Greta as in other measures, and winged spores, Group 7, attain a definite maximum in Tomago Measures.

Fig. 5 may also be regarded as three pairs of small diagrams. Each pair opposite the different coal measures illustrates typical assemblages for Morphological and Ornamentation Groups. In Morphological Groups, the profiles of the three diagrams are similar in essential features. This means that the general assemblage for Morphological Groups is typical in all coal measures, and that the diagram for order of abundance in all measures (Fig. 4) is a characteristic and constant assemblage for the whole of the Permian. Assemblages for Ornamentation Groups are more variable. The profile of Groups 1, 2 and 3 is typical in all three coal measures, but important variations occur in Groups 4 to 7. For example, in Newcastle and Tomago Measures, Group 7 is four to thirteen times more abundant than Group 6, but in the Greta Measures, Group 6 is twice as numerous as Group 7. Similarly in the Tomago Measures, Group 4 is nine times more abundant than Group 5, but in the Greta Measures Group 5 is more numerous than Group 4.

The constant assemblage for Morphological Groups probably has important palaeobotanical implications, but the variable assemblage of Ornamentation Groups would appear to be the more promising in stratigraphical correlation—if certain features in assemblage can be established as characteristic of different coal measures. The higher proportion of verrucate spores, Group 6, in the Greta than in other measures appears to be a typical feature, as it persisted in all samples of Greta coal examined.

#### PALAEOGEOGRAPHICAL DISTRIBUTION OF MICROSPORE-GROUPS IN THE NEWCASTLE MEASURES.

Average percentages are shown in Table 7 for relative abundance of spore-types belonging to all groups in coal samples from the Newcastle Measures throughout different coalfields.

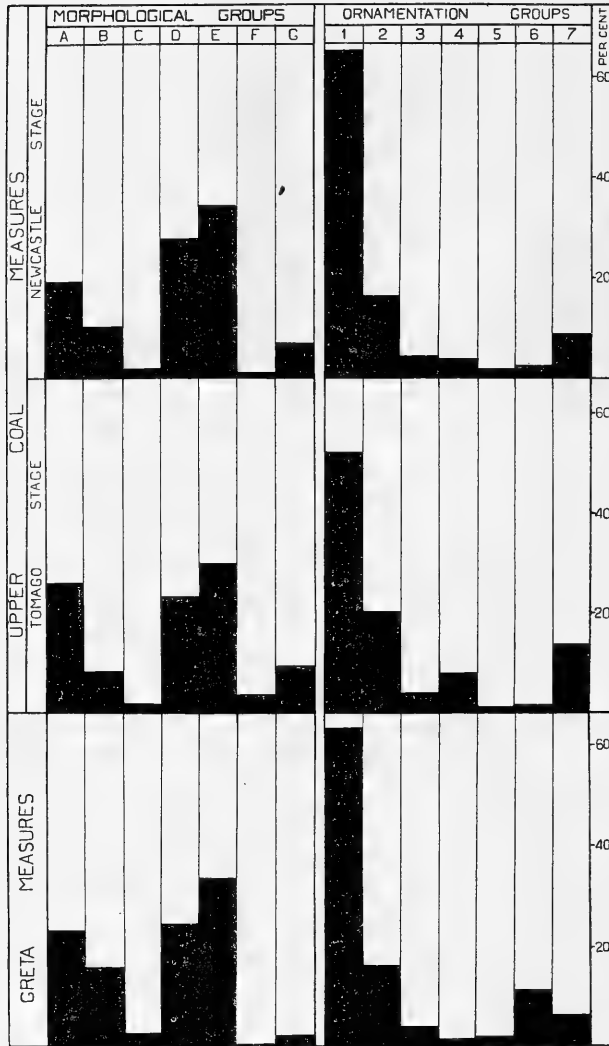


Fig. 5.—Stratigraphical variation in assemblages of microspores belonging to different groups.

Biwinged-monolete spores belonging to Morphological Group G and winged spores of Ornamentation Group 7 are considerably more numerous in the Northern Coalfield than in marginal areas of deposition. All Ornamentation Groups are represented in every coalfield. In the Morphological Groups, the monowinged-trilete spores, Group C, have not been found in the Northern Coalfield, and monowinged-monolete types, Group F, appear to be absent from the North-Western Coalfield.

Apart from the foregoing examples, there is no reliable evidence of definite trends or relations to palaeogeography, although the majority of groups show what appear to be small random variations in abundance from one coalfield to another.

SUMMARY.

Forty-seven representative seam-samples from all measures and fields in the main Permian basin were examined. Microspores were found abundantly in all coals, except those from the South-Coast Coalfield. No variation of special significance is revealed in diversity of types present in different coals. Most abundant spores are all simple forms,

including the smallest of New South Wales Permian types. Lateral variation in abundance of some spore-types in the Newcastle Measures is related to palaeogeography. Of the forty-eight spore-types, thirty-four occur in all measures, and fourteen appear to have limited ranges.

Relative abundance and distribution of spores is considered in terms of morphologically-related groups, and groups with similar forms of ornamentation. Morphological Groups show a typical assemblage in all coal measures, while assemblages for Ornamentation Groups are more variable. Lateral variation in group-assemblages does not appear to be related to palaeogeography.

#### ACKNOWLEDGEMENTS.

The writer wishes to acknowledge helpful discussion with Dr. A. B. Walkom, Director of the Australian Museum, and Mr. F. V. Mercer, Botany Department, University of Sydney, on spore morphology; assistance of his wife in preparing results of spore-counts and diagrams for publication; lettering on diagrams by Miss N. Hinder; and the co-operation of Mining Companies and the New South Wales Department of Mines in obtaining material for microscopical examination.

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ROBIN JOHN TILLYARD.  
1881-1937.

(*Memorial Series, No. 11.*)

(With Portrait.)

Robin John Tillyard was born at Norwich, England, on 31st January, 1881. As a boy he delighted in natural history, taking a special interest in birds and in butterflies and moths. His school days were spent at Dover College, a small Public School, which though of fairly recent foundation, occupies the buildings of an old Priory. Intended for the Army, he passed the Army Examination for Woolwich, but was rejected on medical grounds. On later competing for scholarships for Oxford and Cambridge he won them at both Universities, and, choosing Cambridge, proceeded to Queens' College as a Foundation Scholar.

In 1903 he took his B.A. degree, being placed as Senior Optime in the Mathematics Tripos; he then read Theology for a year, but on realizing that the Church was not his vocation, secured a teaching appointment at Sydney Grammar School as Second Mathematics and Science Master. As a teacher he was supremely successful and is still remembered with affection and gratitude by his former pupils.

In 1909 he married Patricia Craske, an old friend of his Cambridge days, and the first of their four daughters was born at Hornsby, New South Wales, in 1910.

While at the Grammar School his interest in dragonflies developed, his first paper on these insects being published by the Society in 1905. As a result of his increasing preoccupation with natural history he decided to abandon teaching for a scientific career and he resigned his post at the Grammar School in 1913.

He spent the years of 1913 and 1914 as a research student at Sydney University, working under Professor Haswell. In 1914 he was involved in a railway accident, and as a result of the injuries which he sustained, he suffered for the rest of his life from a crippled back. In spite of this setback he was granted a B.Sc. at the end of 1914, this being the first occasion on which the University had conferred such a degree for research.

In 1915 Tillyard was awarded a Linnean Macleay Fellowship in Zoology, which he held for a period of five years, and in 1917 his book "The Biology of Dragonflies" was published by the Cambridge University Press. This book, which still remains unchallenged as the best general work on these fascinating insects, and which had been preceded by the publication of some 46 papers on the same Order, immediately placed Tillyard in the forefront of young zoologists in Australia. During the same year a D.Sc. degree was conferred on him by the University of Sydney, where he was appointed a Lecturer in Zoology, and he was awarded the Crisp Medal by the Linnean Society of London for his paper published by that Society "On the Rectal Breathing Apparatus of some Anisopteroid Larvae".

Two years later, Tillyard undertook his first applied biological problem when he visited New Zealand at the request of the New Zealand Government in order to study and advise on problems associated with the trout fisheries. His report, entitled "Neuropteroid Insects of the Hot Springs Region, New Zealand, in Relation to the Problem of Trout Food", was published by the Society in 1920.

As a direct outcome of his visit to New Zealand, he was offered and accepted the position of Chief of the Biological Department of the Cawthron Institute, at Nelson. This Agricultural Research Institute, which had then only recently been opened, is endowed by funds bequeathed by Thomas Cawthron, a wealthy New Zealand pastoralist.

Before starting work at Nelson, Tillyard visited research organizations in America and England, and on his way to America he renewed his friendship with Frederick Muir, an entomologist employed by the Hawaiian Sugar Planters' Association. Muir was an ardent exponent of the biological control of insects, and there is no doubt that it was his influence which stimulated Tillyard's interest in this field of applied entomology.

In 1920, the year in which he went to Nelson, he was awarded an Sc.D. degree by Cambridge University.

The eight years which the Tillyards spent in New Zealand were undoubtedly the happiest which they enjoyed together as a family. The delightful climate and surroundings of Nelson; the splendid opportunities for research unhampered by excessive administrative duties; the growing sense of progress and achievement; the interest in the activities of their children, all combined to render these years memorable ones in every way.

In 1925 he was elected a Fellow of the Royal Society. In the following year his great work, the "Insects of Australia and New Zealand", was published by Angus and Robertson Ltd., and he again visited England, this time as a representative of New Zealand on the Research Committee of the Imperial Conference. During this overseas visit, Tillyard delivered numerous lectures, principally on fossil insects, which had long been one of his special interests, but also on the biological control of insects and weeds. While on the first topic he spoke as a master, on the second one he was on less sure ground, as although following the successful introduction of an insect parasite of the Woolly Aphis of apple trees into New Zealand, he had acquired great local merit, he was neither by training nor by temperament well equipped as an applied entomologist.

Among the lectures which he gave was the Trueman Wood Memorial Lecture of the Royal Society of Arts, and this lecture, which was delivered to a distinguished audience, gained him the Trueman Wood Memorial Medal. Tillyard, as well as being an excellent conversationalist, was a convincing and dramatic lecturer, and as a result of his campaign in England, he won considerable support for his projects, which involved research, the hoped-for outcome of which was to be the biological control of insects and weeds. He was promised, and later obtained, substantial grants from the newly-constituted Empire Marketing Board, for the purpose of building and equipping laboratories at Nelson.

There is no doubt that after his return to Nelson, following his triumphal tour of Europe and America, Tillyard felt cramped and isolated and in need of a wider field for his endeavours. In 1928 he was approached by the Commonwealth Council for Scientific and Industrial Research and asked to take charge of their developing entomological research activities. At first he demurred, but as a result of a brief visit to Australia he became persuaded, and agreed to accept the position of Chief of the Division of Economic Entomology. Following a short period in Australia, during which he selected a site for a house at Canberra, he again visited America and England, this time in order to recruit staff for the newly-formed Division, and also for the purpose of establishing a working relationship with the Parasite Laboratory of the Imperial Institute of Entomology.

In the eight years which followed, fresh honours came to him; his college at Cambridge elected him to an Honorary Fellowship in 1928; in 1929 he received the R. M. Johnston Memorial Medal from the Royal Society of Tasmania; and in 1935 the Mueller Memorial Medal from the Australian and New Zealand Association for the Advancement of Science. The new entomological laboratory buildings were ready for occupation at the end of 1929, and by 1930 the Division was on its feet and well established, and his staff busy on a variety of problems.

The years at Canberra were not happy ones. The condition of his injured spine deteriorated and he was in almost continuous pain; added to this he was by temperament unsuited to be a Civil Servant. He was disappointed that he was not able to show such rapid results as he had anticipated and had led others to expect; he was worried by personal jealousies and by his relationship with his administrative colleagues. Following a visit to the Pan-Pacific Science Congress in Chicago in 1933 he had a nervous break-

down, and in 1934 he resigned from the Council for Scientific and Industrial Research on the grounds of ill-health.

His last years of life were busy, though restless, and were occupied by a variety of interests to which he transferred his still apparently inexhaustible mental and physical energy. He died on 13th January, 1937, at Goulburn Hospital, at the age of 56, as the result of injuries received in a car accident.

#### *Scientific Work.*

Tillyard's most notable achievement in the field of applied entomology was his successful introduction into New Zealand in 1921 of a hymenopterous parasite (*Aphelinus mali*) of the Woolly Apple Aphis. The Woolly Aphis had previously been a major pest in New Zealand apple orchards and its permanent control by so simple a method earned for Tillyard a great deal of deserved public gratitude.

While in New Zealand he was responsible for initiating several other projects involving the biological control of insects. Some of these, such as the control of the Golden Oak Scale, have proved successful, while others, as for example, the biological control of the introduced European Earwig, failed to give the desired results. Likewise with weeds; whereas the Gorse Seed Weevil (*Apion ulicis*), which Tillyard first introduced into New Zealand, now shows promise of preventing the further spread of gorse, his introduction of the Cinnabar Moth (*Tyria jacobaeae*) for the control of ragwort has served no useful purpose, and his hopes of controlling blackberry, of which he would say there was but a single bush in the South Island of New Zealand and that it was two hundred miles long, were early doomed to disappointment.

When in 1928 he started work with the Council for Scientific and Industrial Research in Canberra, he was still obsessed with the idea that most entomological problems could be solved by biological methods, and in his report on the work of the Division of Economic Entomology for the year 1928-29, he summarized his research programme as "the control of noxious weeds by their natural enemies and the control of insect pests by beneficial parasites and predators". Of recent years the scope of the work undertaken by the Division has broadened very considerably, and though by now several of Tillyard's ambitious, and even sometimes fanciful projects, have long since been forgotten, it is pleasing to be able to record that a problem on which he first became interested in 1926, while still in New Zealand, now, some twenty years later, shows abundant promise of success. This problem was the control, in Australia, of the introduced weed, St. John's Wort (*Hypericum perforatum*), by means of insects, especially leaf-eating beetles.

Although it is impossible to write with enthusiasm of Tillyard's contribution to applied entomology, it is far otherwise as regards other aspects of entomology. He was in every way a great entomologist. In his publications, which comprised nearly 200 papers, he ranged over the whole insect kingdom and described new material in all but a very few Orders. While his interests lay especially with the more primitive groups of insects, he had an unrivalled knowledge of all groups. Apart from his work with the Odonata, his most significant contributions were his series of papers entitled the "Panorpid Complex" and his studies of fossil insects.

Following his early work with dragonflies, he turned his attention to the Neuroptera and the first of his studies of Australian Neuroptera was published by the Society in 1916, and the eighth, and final part, in 1919. In this series of papers he dealt, not only with the classification of the group, but also with their morphology and life-histories. In 1917 his first paper on the Mecoptera was published, an Order which was to hold his interest to the end of his career. The series of papers on the Panorpid Complex was published by the Society in 1918 and 1919. In these papers he opposed Handlirsch's views that the Holometabola had a quadruple origin, and as well as suggesting that the Neuroptera and Mecoptera had much in common, he suggested that the Mecoptera was the central Order from which all the rest of the Holometabola, apart from the Coleoptera and Hymenoptera, may well have been derived. In this series of papers, as well as in others, he set out to make a comparative study of the mouth-parts and other imaginal structures, and as well, the structure of the larvae and pupae. In actual achievement he

seldom progressed further than a study of the wings, but his investigations of the difficult problems associated with wing venation were of such a high calibre that they surpassed all else written by his contemporaries on this topic.

Tillyard's rapidly developing grasp of this aspect of the comparative morphology of insects was to serve him in good stead when he undertook the study of fossil insects, of which, in most instances, little more than the wings are preserved. His first paper on fossil insects was published in 1916 and his last in 1937.

The greater number of his fossil papers deals with the Triassic insects of Queensland, the Upper Permian insects of New South Wales and the Lower Permian insects of Kansas. In the light of more recent knowledge some of his interpretations and deductions, such as those concerning the ancestry of the Hymenoptera, have been shown by others to be incorrect. Nevertheless, regarded as a whole, his long series of papers dealing with these three separate faunas represents a brilliant and outstanding contribution to a difficult and fascinating field of study.

It was to be expected that Tillyard's interest in extinct groups of insects, and in primitive insects, would induce him to ponder the problem of the origin of insects, and in 1930, he chose as his subject for the Presidential Address to Section D of the meeting of the Australian and New Zealand Association for the Advancement of Science, at Brisbane, "The Evolution of the Class Insecta". In this lecture, which was published later the same year in an extended form in the *Proceedings of the Royal Society of Tasmania*, he put forward an ingenious but unnecessarily complex hypothesis. Having reached the conclusion that insects must have been derived from the Symphyla, he attempted to explain how progoneate Symphyla and opisthgoneate insects can have been derived from a common ancestor, and in both instances suggested that post-cephalic somites had been added by anamorphosis.

Another subject which interested him was the origin of the insect fauna of Australia and New Zealand, and no man was better fitted to write on this topic.

Tillyard was a keen angler, and to this may be ascribed his interest in the Ephemeroptera, Perlaria and Trichoptera, in all of which groups he produced, not just short papers containing brief descriptions, but revisions which were monographic in scope. While his book on the insects of Australia and New Zealand owed much to the co-operation of friends, it was entirely original in conception, and will long remain a monument to his vast knowledge and great energy. It has earned him the gratitude of all Australian entomologists as well as that of workers in this field in other countries.

A lesser known book was published in 1936 and dealt with the supposed Pre-Cambrian fossils from the Adelaide Series in South Australia. These fossils were claimed by Sir Edgeworth David and by Tillyard to be the remains of the oldest forms of life as yet discovered, and were said to represent a new Class of Arthropods, the Arthrocephala, of which Tillyard described two species.

Tillyard's early training had been as a mathematician; he taught mathematics for some years and he retained his interest and grasp of the subject long after he gave up teaching. It is thus surprising to note that he never made use of mathematics in any of his biological work.

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Tillyard was a man of vivid personality and wide interests. All that he did was done with evident relish and enjoyment, and with great and infectious enthusiasm. He was of a mercurial disposition, and though most often he was engaged in following some interest with intense keenness, there were times, when due to severe pain, his spirits sank to their lowest ebb. He enjoyed people and personal contacts and was especially happy and stimulated when talking on some topic to an appreciative audience, whether to a few people gathered around him or to a packed lecture theatre. As well as being a brilliant conversationalist, he was an excellent lecturer, since he was a confident, fluent speaker with a good command of words. His presentation was somewhat dramatic and he did not hesitate to draw, while lecturing, on his vivid imagination.

Few men with so many calls on their time contrive to be such good correspondents. His letters were not just brief accounts of doings and happenings, but were full of interest, and were vivid expressions of his personality and intense vitality.

He had numerous hobbies of which perhaps gardening took pride of place, and he delighted in growing rare and unusual plants, especially those native to Australia and New Zealand. For him no garden was complete without a pond over which his beloved dragonflies could dart and hover. He took a great interest in all animals, and there were seldom periods when wallabies, 'possums and tame lizards and magpies were not to be found in his garden. He was at his best in the bush, when laden with collecting equipment, his keen eyes noting everything of interest, he would talk with equal knowledge on both insects and plants. Always encouraging to young biologists and to others with but little knowledge of his favourite subjects, he would take infinite pains to answer questions in clear and simple language.

In spite of his frail physique and poor health, he had great staying powers, and when his interests were involved, his mind would overcome all his physical disabilities and very often, when out on expeditions in the bush, he would outlast seemingly more vigorous men.

Although his health prevented him from taking part in active games, he played tennis up to 1928 and he took an interest in games, especially in cricket and tennis. Nothing gave him more pleasure than to see his daughters excel at sport, and many will remember the intense excitement he displayed while watching hockey matches in which his girls were playing. He took a great pride in his family and in all its doings.

As a host he excelled, and those who were privileged to attend seminars at his house, or to visit it for tea on Sunday afternoons, will remember the friendly and stimulating atmosphere of his home.

Tillyard had the spiritual side of his nature highly developed and he was a regular church-goer. He once wrote a hymn, for which he also composed the tune; he also wrote a novel, but this was never published. His interest in Psychological Research, which extended over many years, was pursued with the same fearless vigour that he gave to all his undertakings. Although advised by several friends to desist from following up his investigations in this direction, he remained undeterred, and in 1928 published in *Nature* an account of what he considered to be evidence of the survival of human personality following physical death.

He had a keen sense of civic responsibility, and both in Nelson and in Canberra, supported all causes having as their object the furtherance of the well-being of the community. He served on the Council of Canberra University College and was most anxious that Canberra should become a University centre. The *Australian National Review*, of which he only lived to see a few numbers issued, was one of his interests, and not only did he act as joint-editor of this Review, but he was also partly responsible for its inception.

All those who knew Tillyard, and he had a very wide circle of friends in all walks of life, will need no reminder of his personality. Although a decade has passed since his death, his memory remains a vivid picture, for his mental alertness, ready wit and puckish humour were unique. They will remember him, too, as a stimulating friend and companion, and if he was perhaps somewhat egocentric, this was but a single facet of a great character.

No account of Tillyard's life would be complete without some mention of the part played in his career by his wife. His debt to her was incalculable. During the period when he was at Sydney University studying for his B.Sc. degree, the Tillyards were in difficult financial circumstances, and it was entirely due to Mrs. Tillyard's devotion and encouragement and to her sheer hard work, that her husband was enabled to complete his studies and to bring them to such a successful conclusion. Not only did she nurse him through long and distressing illnesses, help him in his work with her criticism, and also by illustrating in colour his articles on insects in the *Australian Encyclopaedia* and in his other books, but she was a constant and unswerving support to him when he was overcome by periods of deep depression. She shared his many interests, not merely as a passive onlooker, but as an active participator, and it can be truly said that it was to his wife above all that he owed not only his happy home life, which meant so much to him, but also all his success.



## DESCRIPTION AND LIFE HISTORY OF A NEW WESTERN AUSTRALIAN COCCID.

By J. R. T. SHORT, B.Sc., Demonstrator in Biology, University of  
Western Australia.

(Communicated by Dr. A. J. Nicholson.)

(Nineteen Text-figures and one Map.)

[Read 27th November, 1946.]

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I. INTRODUCTION.

In September, 1945, it was brought to the notice of the Department of Biology, University of Western Australia, that an infestation of Coccid galls was seriously hampering the establishment of Tuart (*Eucalyptus gomphocephala*) plantations on Rottneet Island.

Since the Tuart gall is exceptionally rare on the mainland, it was suggested that the reason for the unduly large population of Coccid galls on Rottneet Island might lie in the fact that parasitoids of the Coccid were either not present or not proving a limiting factor. Accordingly, an investigation was undertaken to explore the possibilities of biological control of the Coccid pest through the introduction to the island of a parasitoid or of parasitoids. It was obvious that the first step in such an investigation should be a research into the ecology of the gall in order to determine the effect of natural enemies; and that basic to this ecological enquiry would lie an investigation into the general morphology and life history of the insect.

This paper, then, represents an attempt to establish a basis for the above investigation. The Coccid proved to be a new species of the genus *Apiomorpha* Rùbs. (*Brachyscelis* Schrader).

II. HISTORICAL.

The genus *Brachyscelis* was established by Schrader in 1863. Schrader (1863*b*, p. 6) defined it as follows:

"Genus *Brachyscelis*. Where the females have six legs complete, but short, and unfit for use."

Schrader shortly afterwards (1863*c*) discussed the subject further and described five specimens taken in the neighbourhood of Sydney.

In 1894, C. H. Rùbsaamen re-established the genus as *Apiomorpha*, stating the characters as follows:

"Adult females pear shaped, the abdomen tapering, and ending in two strongly chitinous tubercles. Mouth parts small, more or less atrophied. Feet and antennae present in all stages but more or less atrophied in adult. Anal ring with six hairs. Inhabiting woody galls of characteristic shapes, whose growth at the expense of their host they cause and direct.

"Larvae ovate and segmented; abdomen ending in two suppressed tubercles each bearing a long seta. Margin of body surrounded with fringe of uniform acuminate spines, each of which bears for a little while after birth, on either side, thin, hyaline, wing-like appendages; each species apparently bearing the same number. Males undergoing their transformation in separate cylindrical galls."

This writer described and figured five species of the genus.

The new species conforms with the characters stated by Rbsaamen with the exception of the wing-like appendages of the larva, the presence of which I did not detect, and the more or less atrophied mouth parts. This, I believe, may be due to the fact that in the Coccidae the stylets may be withdrawn from the plant and looped within the body, thus not being visible externally.

A great deal of our knowledge of the genus *Apiomorpha* is due to the work of W. W. Froggatt. His first paper on this subject appeared in 1892.

In 1893, J. G. Tepper proposed a new classification for the family Brachyscelidae and described new species in a paper which was severely criticized by Froggatt the following year.

Between 1893 and 1898, Froggatt published four papers on the family Brachyscelidae with descriptions of new species.

C. Fuller (1896 and 1897) described new species in the *Agricultural Gazette of New South Wales* and in the *Journal of the West Australian Bureau of Agriculture*. In 1899 he published an amplification of these papers, and described another new species.

Three more species were added to the genus in 1921 with Froggatt's "Descriptive Catalogue of the Coccidae of Australia". In the years 1929 and 1930, this writer published two further papers on gall-making Coccidae in which he described six new species of *Apiomorpha*.

Froggatt's work culminated in 1931 with his "Classification of Gall-making Coccids of the Genus *Apiomorpha*". This classification I have followed in making my determination of the new species.

### III. SYSTEMATIC POSITION.

The classification of Froggatt is based upon the structure of the female galls, the arrangement of the hairs (setae) and spines on the dorsal surface of the female, and the form of the anal appendages.

Froggatt separates the species of *Apiomorpha* into nine groups, of which the new species herein described clearly falls into his Group D, defined as follows:

"Galls oval, smooth or fluted, sessile, apical orifice small circular. Normally produced upon the branchlets, but often growing out of flower buds. Coccid with the dorsal surface covered with scattered thorn-shaped spines. Anal segment longer than broad, anal appendages coalescing with anal segment, which is broad at the base, round and rugose at the sides, and with the anal appendages forms a lance-shaped tip which is slightly bifid."

The new species conforms with all the above characters with the minor exception that it has never been observed growing out of flower buds.

Within this Group, the new species shows many features of likeness with *Apiomorpha ovicola* (Schrader, 1863a). As with this species, the whole body surface is clothed with long attenuated hairs. Also, dorsally, the central areas of the cephalic and thoracic segments are covered with curved thorn-shaped spines. However, with *A. ovicola*, the fourth to sixth abdominal segments are, according to Froggatt, covered with these spines; whereas the new species shows on the third to fifth abdominal segments but one row of spines on the posterior margin of the segment together with several scattered spines. The sixth abdominal segment of the new species possesses a semicirclet of spines on its posterior margin and several (often but two) medially-placed spines.

The anal region differs also in that the anal segment is longer and the anal appendages but very slightly bifid; thus this segment plus its appendages exhibits a much more slender shape than is the case with *A. ovicola* as figured by Schrader (1863a) and Froggatt (1931).

With reference to the shape of the female gall, this shows a marked similarity to that of *A. glabra* described and figured by Tepper (1893); and Fuller (1899) reports having seen *A. glabra* in Western Australia.

Tepper's (1893) description of this species is as follows:

"Female Gall. Solitary, sessile, considerably projecting beyond point of attachment posteriorly, ovate, nearly smooth, faintly striated longitudinally, and sometimes with irregular, smooth warts (male galls?), whitish or grey, clouded with brown; apex rounded, aperture very minute; cavity rather large, corresponding in form with external shape. Insect not known, nor male galls.

"Length, 28 mm.; diameter over attachment, 15 mm.; at apex, 3.5 mm.

"Habitat—Mount Lofly Ranges, Lyndoch, etc. On stout branches of *Eucalyptus rostrata*, but rather rare and always solitary. The outer texture resembles that of the bark of the branches very closely."

There is obviously a stronger possibility that the new species described is Tepper's *A. glabra*, but since he has described neither the female insect nor the male gall, his species cannot be regarded as valid.

Froggatt (1893), however, states that he considers *A. glabra* an abnormal form of *A. ovicola*. The shape of the gall figured in this paper is typical of some five hundred examined on Rottnest Island and ten collected upon the mainland—always upon *Eucalyptus gomphocephala*. Hence it would appear that this is no mere abnormality, but the normal form of the gall of the species, and the gall of the new species is much more elongate than that figured by Schrader (1863a) for *A. ovicola*.

To the remaining species of Froggatt's Group D, *A. helmsi* (Fuller), *A. withersi* (Frogg.) and *A. floralis* (Frogg.), the new species shows no close resemblance.

The Coccid described in this paper, then, cannot be referred to any species yet described. The new species, *Apiomorpha egeria*, is therefore erected for its reception.

Types, male and female, and male and female galls, have been placed in the Australian Museum, Sydney, New South Wales.

#### IV. DESCRIPTION OF MALE AND FEMALE IMAGOS AND GALLS.

##### APIOMORPHA EGERIA, n. sp.

In the following descriptions, measurements refer to type specimens only and their exact values have no specific significance.

*Male Imago.* Figs. A-F.

Length, body (to extremity of genital sheath) 2.55 mm. Length, forewing 2 mm.

Colour: Chiefly bright yellow; ocelli deep purple.

Forewings whitish and opaque; haltere light brown; genital sheath light brown.

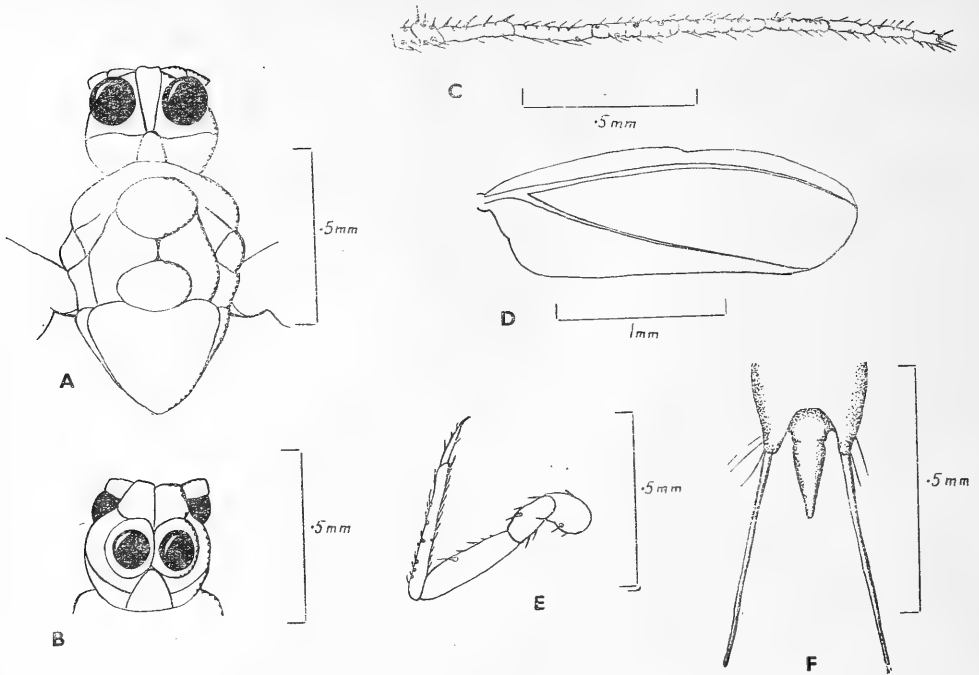
Head globular, narrower than prothorax with four large ocelli.

Antennae (length 1.57 mm.) 10-jointed, these joints being neither distinct nor regular, two basal segments globular, and approximately equal in size; third, fourth, fifth and sixth segments elongate, and thrice the length of basal segment; seventh, eighth, ninth and tenth segments decreasing in size in this order, eighth segment being twice length of basal segment; all segments with numerous small setae, apical segment surmounted by cirlet of larger setae.

Forewings membranous, showing veins R and M, and possessing a uniform covering of microtrichia; halteres minute, slender, method of attachment to pocket of forewing indiscernible.

Legs: Coxa globular; trochanter elongate showing suggestion of division, length of coxa in relation to trochanter with proportion 2:3; femur stout, twice length of trochanter; elongate slender tibia with length in relation to trochanter with proportion 5:3; tibia with small apical spur; slender, single-clawed, tarsus, approximately one-third of length of tibia; all segments with numerous small setae.

Terminal abdominal segment with two lateral lobes each bearing an elongate white filament (length 3.4 mm.), genital sheath slender, conical.



Figs. A-F.—*Apimorpha egeria*, n. sp. A. Head and thorax of male imago, dorsal view. B. Head of male imago, ventral view. C. Left antenna of male imago. D. Forewing, male imago. E. Right mesothoracic leg of male imago. F. Eighth abdominal segment and aedeagus sheath of male imago, dorsal view.

*Female Imago.* Figs. G-K.

Length, body 2.43 cm.; maximum body width 1.32 cm.; shape turbinate; integument covered with scattered attenuated setae; body covered with white mealy secretion; integument membranous; antennae, legs and spiracles chitinized, anal appendages strongly chitinized.

Colour: body uniformly creamish-brown; antennae light brown; pro-, meso- and meta-thoracic legs red-brown with colour deepening in this order; colouration of individual leg lightest at basal segment, darkening towards apex; spiracles red-brown and anal appendages a very dark brown; setae of integument light brown and spines a deep red-brown.

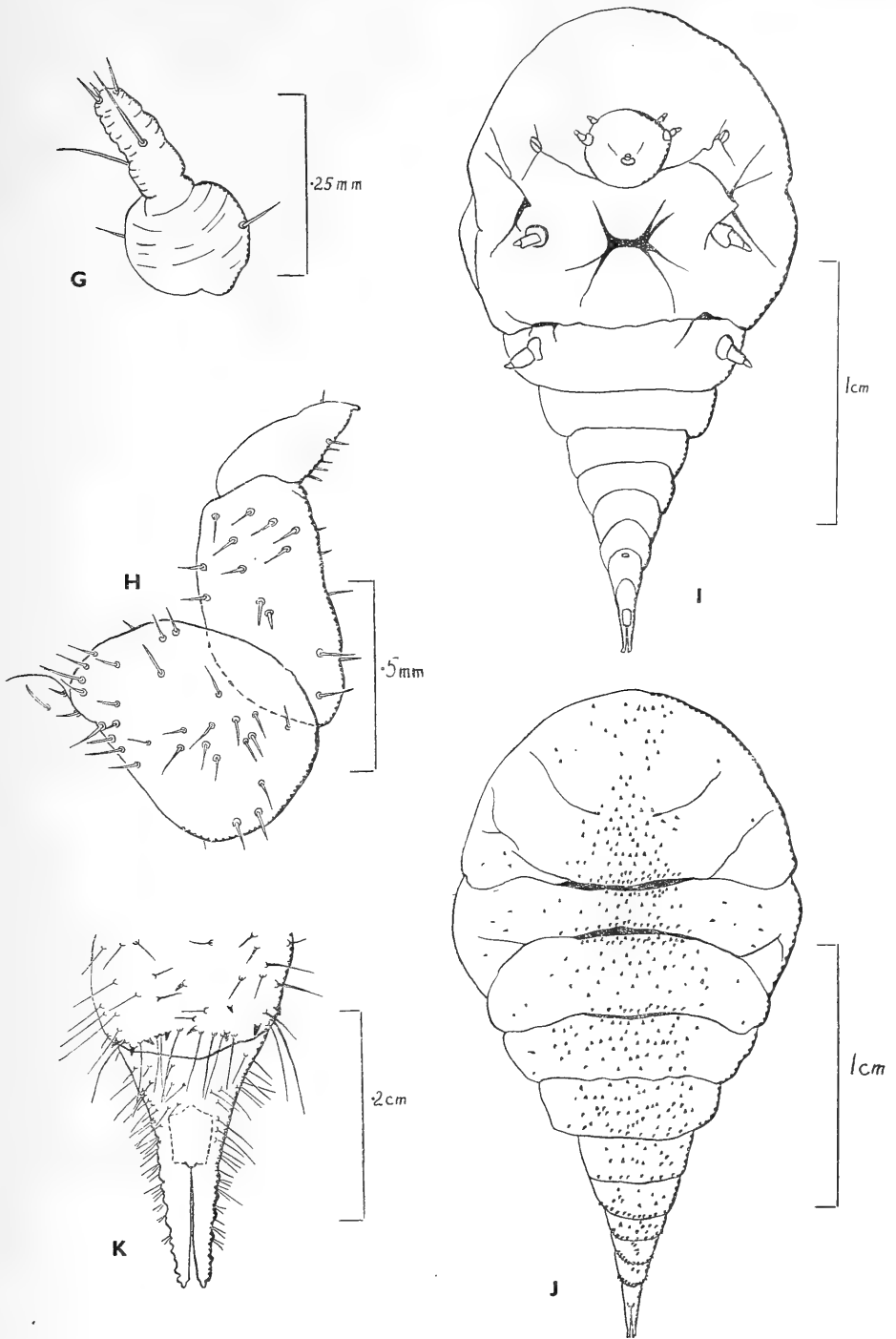
In this description, I think it preferable to reverse the usual procedure and describe the ventral surface before the dorsal in order that attention may be concentrated on the taxonomic details of the dorsum.

*Venter.*—Head coalesced with first two thoracic segments; eyes absent; antennae two-segmented, basal segment broad, globular and shorter than wide; apical segment more elongated, twice length of basal segment, cylindrical, annulated, rounded at apex and surmounted by a circlet of setae; mouth a small circular aperture situated on a convex circular area of integument; mouth parts always looped within body when insect examined; labium minute, semi-circular, one-jointed.

Prothoracic leg, three-segmented, basal segment squat, much broader than long, second segment large, width one-half of basal segment, but longer than this segment; apical segment bluntly conical, length approximately half that of basal segment; apex annulated and bearing a small, medially-directed claw.

Head plus first thoracic segment separated from mesothorax by a deep median cleft, terminating at the level of and anterior to the mesothoracic spiracles.

Mesothorax very broad with a deep infolding of integument in centre; mesothoracic leg having same proportion as prothoracic leg, but larger, more heavily chitinized.



Figs. G-K.—*Apiomorpha egeria*, n. sp. G. Left antenna of female imago. H. Right mesothoracic leg of female imago. I. Female imago, ventral view. J. Female imago, dorsal view. K. Anal appendages of female imago, dorsal view.

Metathorax sharply demarcated from fused cephalic and pro- and mesothoracic segments by a deep intersegmental fold in which are situated the metathoracic spiracles. Metathoracic legs similar in proportion to mesothoracic, larger, more heavily chitinized.

Abdominal segments distinct, seven in number, tapering in width, length of segments relatively constant; aperture of vagina in median anterior position on sixth abdominal segment; seventh segment (anal) long, narrow, tapering, coalesced with base of anal appendages, somewhat rugose, carrying short, fine setae springing from small bosses; fringed anal ring situated mid-ventrally; anal appendages long, slender, markedly rugose, with tips but slightly bifid. Abdominal spiracles absent.

*Dorsum*.—Proportion of segments as for venter, but pro-, meso- and metathoracic segments distinctly marked by means of deep median intersegmental clefts.

Median surface of head and of thoracic regions covered with enlarged, red-brown, thorn-shaped spines (the rose-shaped thorns of Froggatt), which have a much greater density in the intersegmental regions; first and second abdominal segments possessing uniform bands of spines extending almost across the dorsal surface; third, fourth and fifth abdominal segments possessing a row of spines across their posterior margin, together with several scattered spines; sixth abdominal segment with semicircle of spines on its posterior margin, and several (often two) medially placed spines; anal segment entirely lacking spines, but setose especially laterally.

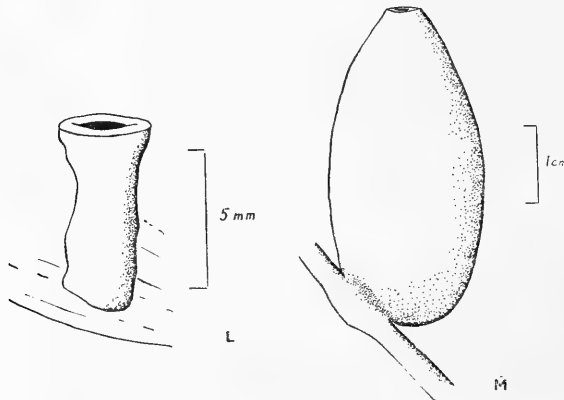
The third instar female immediately following completion of the second ecdysis shows considerable differences in size and proportion in comparison to the gravid female. Length 0.95 cm. Width 0.49 cm.

It is notable that the female of this earlier period of the third instar shows integumentary setae in much greater density than was the case with the gravid female.

*The Male Gall.* Fig. L.

Small, length 0.8 cm., width 0.3 cm.; with general cylindrical shape and dilated apex; colour predominantly purplish in younger stages before apex opens, later becomes green, although young stages sometimes exhibit a green colouration.

Generally situated on adaxial surface of leaves, but may be found on abaxial surface, on branchlets, and rarely on the sides of the female gall.



Figs. L-M.—*Apiomorpha egeria*, n. sp. L. Male gall. M. Female gall.

*The Female Gall.* Fig. M.

Although the female galls on Rottneest Island are distinctly gregarious, it would appear that this is but a result of undue numbers; on the mainland, galls are solitary.

Length 4 cm., width 2 cm.; gall sessile, ovate, smooth, green (this colour tending to brown with age); apex slightly depressed with a small circular orifice; wall of gall consisting of two distinct regions, the outer thick and spongy and the inner hard and thin; situated on branchlets, or, rarely, on stem.

## V. IMMATURE STAGES.

*Larva—First Instar.* Figs. N, O.

At this stage it was not possible to differentiate between male and female.

Length (exclusive of antennae and terminal setae), 0.4 mm. Width (exclusive of supra-marginal setae), 0.25 mm.

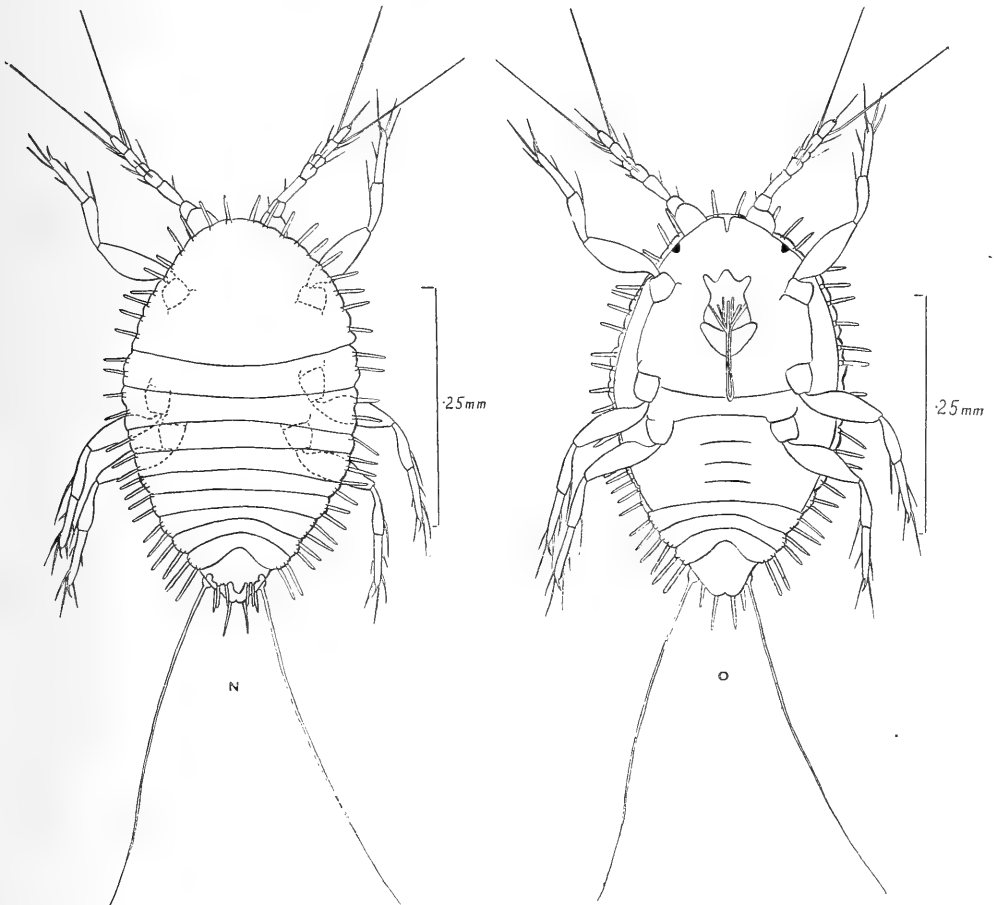
Form oval; dorsum slightly convex; colour yellow with black ocelli.

*Dorsum.*—Head fused with prothorax; meso- and metathoracic segments distinct; seven abdominal segments demarcated and a highly modified apical segment bearing four setae; body surrounded by fifty-eight marginal setae; apical segment bears dorso-laterally two greatly-elongated terminal setae, approximately equal in length to the body.

*Venter.*—Deep cephalic notch situated antero-medially; head, pro- and mesothorax appear as fused, metathorax distinct; abdominal segments distinct, but with first four abdominal segments, the intersegmental suture is only visible medially.

Ocelli-black, situated antero-laterally.

Mouth parts of typical form; maxillary and mandibular stylets elongated and thread-like; beak apparently one-segmented, stout conical; framework of mouth parts large and placed between prothoracic legs.



Figs. N-O.—*Apiomorpha egeria*, n. sp. N. Larva, dorsal view. O. Larva, ventral view.

*Male, Second Instar.* Fig. P.

Body colour white; setae light brown; ocelli black. Length (excluding setae at apex of abdomen) 1.02 mm. Width 0.56 mm.

*Dorsum*.—Head semi-circular and fused with prothorax; two ocelli present; meso- and metathoracic segments broad and flattened.

Abdomen consisting of eight segments tapering to small trilobed apical segment; fifth and sixth abdominal segments bearing dorso-laterally a pair of enlarged setae of length equal to half that of segment, seventh abdominal segment with two pairs of setae more medially placed; each lateral lobe of eighth segment bearing a seta equal in length to the three posterior abdominal segments and elongated in the antero-posterior axis, a pair of small setae medially convergent with those of the corresponding lobe, together with several laterally placed setae; median lobe probably representing the genital sheath visible in the imago enclosing the aedeagus.

*Venter*.—Head and prothorax appear as fused; antennae visible as small blunt antero-lateral elevations; prothoracic legs indistinctly four-segmented, consisting of squat basal segment, and two quadrate segments followed by an elongate, conical, apical segment, of the same length as the three previous segments and surmounted by two short setae; mouth situated on circular elevation consisting of a posterior crescentic labium and a smaller anterior labrum.

Meso- and metathoracic segments distinct, with legs having same proportion as those of prothorax but larger.

Eighth abdominal segment as for dorsum, but median lobe more prominent from ventral view.

*Male Propupa*. Fig. Q.

Length, body 2.04 mm. Width, body 0.68 mm.

Colour: Uniform pale yellow.

Head globular, indistinct from prothorax; antennae short, stout, non-segmented, curved beneath body to base of prothoracic leg.

Meso- and metathorax indistinctly separated; forewing sheaths prominent, stout; legs indistinctly four-segmented.

Abdomen 8-segmented, apical segment consisting of two lateral lobes each bearing an enlarged elongate seta approximately equal in length to the eighth abdominal segment, and the medially-situated genital sheath (visible only ventrally).

*Male Pupa*. Fig. R.

Length, body 2.28 mm. Width, body 0.8 mm.

Colour: Pale yellow, ocelli dull black.

Head distinct from thorax and showing dorsal and ventral ocelli; antennae long, curved beneath thorax, apex free, indistinctly ten-jointed.

Prothorax distinct, meso- and metathorax fused; forewing sheaths large, distinct; legs indistinctly four-segmented.

Abdomen eight-segmented, each segment dorsally bearing a row of setae along its posterior margin; eighth segment consisting mainly of the two lateral lobes each bearing an enlarged elongate seta of approximately the same length as this segment and a stoutly conical genital sheath.

*Female, Second Instar*. Fig. S.

Length, 0.54 cm.; width, 0.23 cm.

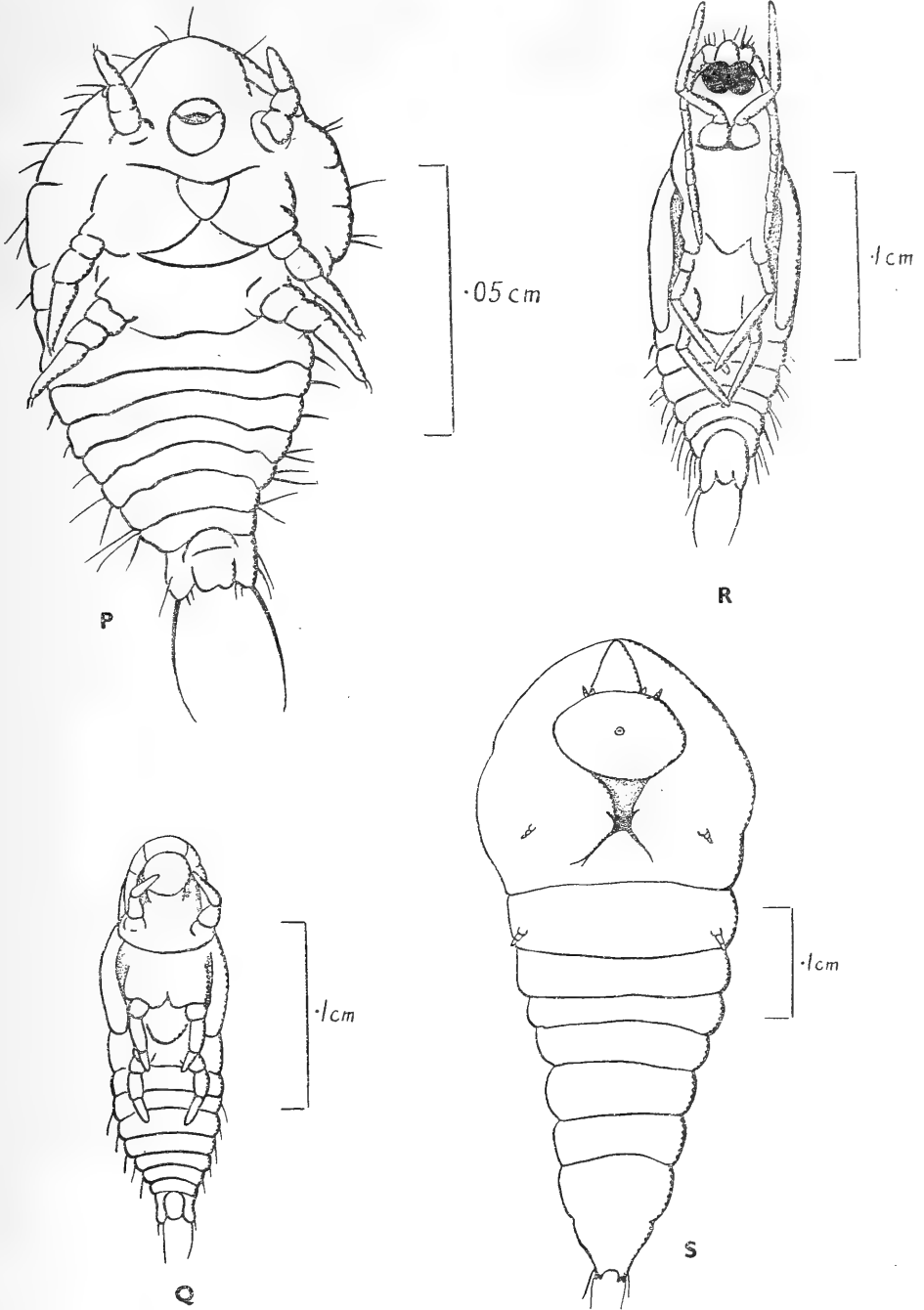
Turbinate in outline.

Body colour white; legs light brown; antennae white; body very lightly covered with light brown setae; spines dark brown.

*Dorsum*.—Head and prothorax fused into a rounded conical mass. Meso- and metathoracic segments distinct. Seven abdominal segments visible gradually tapering posteriorly, the sixth being bluntly conical in form and the seventh crescentic, both with apices directed posteriorly; fifth and sixth abdominal segments each bearing a pair of posteriorly-projecting spines; seventh segment terminating in two tubercles, each of which bears two spines; at the base of each tubercle arises a seta of length approximately thrice that of the spines.



*Venter*.—Head, pro- and mesothorax appear as fused; metathorax distinct; first five abdominal segments distinct, sixth and seventh abdominal segments indistinctly separated.



Figs. P-S.—*Apimorpha egeria*, n. sp. P. Male, second instar, ventral view. Q. Male propupa, ventral view. R. Male pupa, ventral view. S. Female, second instar, ventral view.

Antennae two-segmented, minute. Legs three-segmented, small, increasing in size in series prothorax, mesothorax, metathorax. Mouth situated on raised elliptical fold, anterior to which there is situated a triangular elevation, beginning at the base of the antennae and prothoracic legs, and with apex directed anteriorly. In the mesothoracic region the meeting of two large lateral folds of the integument with a small anterior and a small posterior fold, causes a deep median cleft.

#### VI. LIFE HISTORY.

The emergence of the larvae from the small circular orifice at the apex of the gall was observed to commence in the month of October, and to last for several days with the individual gall, this emergence being accelerated by sunlight. Emergence of larvae from the galls studied at Rottnest Island continued until late in the month of December.

*A. egeria* was found to be viviparous, the larvae emerging in an adhering chain, each larva being covered by a delicate, transparent hatching membrane (Weber, 1930, p. 356). Some seconds after emergence, the larvae shed this membrane and remained for several minutes in a semi-dormant condition at the base of the gall, the interior of which appeared to be a writhing mass of larvae. They then left the gall and travelled rapidly over the surface and along the branchlets to the growing tips. It is of interest to note the observation of Davidson\* on aphids, that the cell sap of the young growing tissue of the host plant is of a very definitely higher nutritive value as food than the older tissues. This, together with the soft nature of the growing parts, will explain the preference of the *Apiomorpha* larvae for the younger plant tissues.

Those which are apparently male larvae took up position on the leaves and appeared to flatten themselves into, and adhere to, the surface of the leaf. The same process has been observed with the female larvae on the branchlets. At this stage, apparently, irritation, resulting from the larvae feeding, caused the galls to commence growth. The botanical aspect of these remarkable objects is admirably described by E. Küster (1937).

The estimation of instar duration was most difficult, the insects being continuously encased in their dense galls. Also the period of duration of the instar appeared to be most irregular, depending seemingly on the rate of growth of the gall. The first instar in both male and female was found to be generally of some ten weeks' duration, though often longer; the second instar duration of the female was observed to be some eight weeks, as was the duration of the second, prepupal and pupal instars of the male collectively. The male imagos first emerged around the 9th February, but were not observed in any numbers until later in this month. The male galls become open at the apex to allow the emergence of the male imago, this process occurring with the abdominal region foremost, and the forewings extended over the head. Fluttering its wings in short spasms, the male flies but feebly and for the most part makes its way to the female gall by crawling fairly rapidly over the branchlets. Impregnation of the female has been observed to occur through the apical orifice of the gall; and soon after the act of impregnation the males apparently die, for when kept in glass tubes males were observed rarely to live for more than one day.

The difference in the duration of the life cycle of the male and female insects is most marked. Since the final instar of the female lasts from February to October-November, the life cycle is annual, but the cycle of the male is of five months' duration only.

The death of the female imago was noted to occur after the emergence of the larvae, the female being left a shapeless mass of derm at the base of the gall.

#### VII. NOTE ON THE ECOLOGY OF THE GALL.

As has been noted previously, *Apiomorpha egeria* has only been observed parasitizing *Eucalyptus gomphocephala*. It would appear possible that this Coccid is confined to but one species of Eucalypt, this surmise being supported by a survey conducted over the major regions of the Tuart forest of Western Australia.

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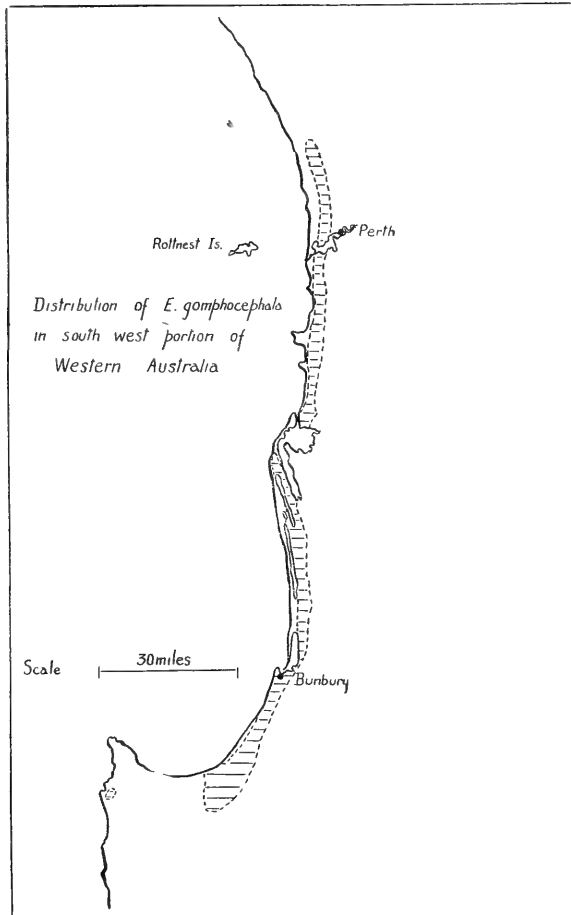
\* Quoted by Imms, A. D., 1931, Recent Advances in Entomology, p. 210.

Gardner (1942) states that the Tuart forest: "is a type of savannah forest in which the trees of the Tuart (*E. gomphocephala*), attaining a height of 40 metres, dominate the forest in almost pure strands, being only rarely associated with such species as *E. calophylla* and *E. cornuata*. It is edaphically confined to the littoral limestone of the Western coastal plain, the range of the species extending from near the Hill River to the Sabina River near Busselton. It is only in the southern part of its range, where the summer (November–April) rainfall exceeds 125 mm. that it attains to the proportions of a forest in its species."

The Tuarts of Rottnest Island are an introduced flora. A map showing the distribution of *E. gomphocephala* in Western Australia accompanies this paper (see Map 1).

The galls of *Apiomorpha egeria*, n. sp., seldom occur on the mainland, and those few taken, both male and female, are, with rare exceptions, heavily parasitized, the main parasite of the female being an Encyrtid Chalcidoid. By contrast, the population of galls upon the Tuart plantation of Rottnest Island is most dense; both female and male Coccids were observed to be extensively parasitized on this island, but apparently not to a sufficient extent to be a factor controlling their undue numbers. The Encyrtid Chalcidoid is absent from Rottnest Island.

Several other species of insects are found associated with the galls, probably as inquilines; these, together with parasitoids, furnishing an extensive ecological complex.



Map 1.—South-west portion of Western Australia showing distribution of *Eucalyptus gomphocephala*.

The action of a species of Chalcidoid (possibly an inquiline) on the tissue of the gall is such as to cause small tubercles to develop on the surface, and frequently greatly to distort the shape of the gall.

Upon the death of the female due to natural causes or otherwise, the gall is found inhabited by Araneida, by small Formicid colonies or by a species of mould.

As was noted in the introduction, it is proposed to deal in detail with the ecology of the gall of *Apiomorpha egeria* in a later paper.

#### VIII. METHODS.

In order to determine the arrangement of the setae and spines on the dorsal surface of the integument, I have followed the method described by Froggatt (1931) in boiling the female Coccid in 10% caustic potash, washing out the contents of the body and then treating the body with spirits of wine, chloroform and turpentine. The required surface of the integument I then mounted in gum chloral. Staining was not necessary.

Injected female imagos, second instar females and second instar, prepupal and pupal males were preserved in museum fluid—a 5% solution of formalin in 70% alcohol (using 19 parts 70% alcohol to 1 part of formalin) with 5 c.c. of pure glycerin added to 100 c.c. of this solution.

Second instar, prepupal and pupal males were also mounted by Britten's Method (utilizing glacial acetic acid, clove oil and euparal). Larvae were stained and mounted in picric acid in polyvinyl alcohol, this mountant being an invaluable aid in the discrimination of detail.

Male imagos were fixed in Bles Solution and stored in 70% alcohol, mounted in gum chloral or in picric acid in polyvinyl alcohol, or by Britten's Method. Of these methods of mounting, none was entirely satisfactory; gum chloral was found to over clear; picric acid in polyvinyl alcohol supplanted the natural colouration with its own green colouration; and Britten's Method, though excellent, is laborious.

The life history of the Coccid was first determined from specimens taken at Rottneest Island. Here, in the month of December, it was possible to obtain female specimens in all stages of development, thus revealing the three instars of the female. Two instars of the male were likewise obtained at this time, and the remaining prepupal, pupal and imaginal instars on the 10th of the following February.

Early in October, 1945, larvae were released upon Tuart trees in the grounds of the Department of Biology, Crawley, thus enabling a verification of the previous observations regarding the number of instars made with Rottneest material. Larvae were also released upon a Jarrah (*E. marginata*) tree in the grounds of the Department, in order to determine whether *Apiomorpha egeria* was capable of parasitizing a Eucalypt other than the Tuart. No galls were observed to develop, but this experiment must be regarded as inconclusive, since the larvae were released late in their season (December), and upon an old tree.

#### IX. ACKNOWLEDGEMENTS.

The author wishes to express his indebtedness and gratitude to Professor G. E. Nicholls and Mr. E. P. Hodgkin for guidance, and to Mr. G. G. Smith for assistance with literature on the Tuart.

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NOTES ON THE GIPPSLAND WARATAH (*TELOPEA OREADES* F.v.M.), WITH A DESCRIPTION OF A NEW SPECIES.

By EDWIN CHEEL.

(One Text-figure.)

[Read 25th September, 1946.]

In these PROCEEDINGS (lvi, 1931, xl), specimens of *Telopea oreades* F.v.M., which were collected at Bombala, N.S.W., were exhibited and recorded, and erroneously classified as the "Tasmanian Waratah", *Telopea truncata* R.Br. (see the *Sydney Morning Herald* for 16.xi.1931 and 21.xi.1931). Specimens were also shown at the same meeting, which although somewhat resembling the Tasmanian species in foliage, were regarded as sufficiently distinct from both *T. truncata* and *T. oreades* to be ranked as a new species. It will be noted that the latter was recorded by Maiden (1911) as *T. oreades* from the Braidwood district, New South Wales. The illustration in Maiden's Forest Flora under *T. oreades* depicts, in fact, only a solitary leaf of that species (Pl. 163, fig. N), which was originally described by Mueller (1860) and later by Bentham (1870). A later description by Mueller (1887-1888) reads as follows: "Finally quite arborescent; branchlets also glabrous; leaves large, firm, mostly obovate-lanceolar entire, their ultimate venules subtle; corolla crimson, slit unilaterally; glandule at the upper end of stalklets rather conspicuous". Moore and Betche (1893) recorded the species for "Coast district, from Moss Vale to Victoria" with the common name "Gippsland Waratah".

The remaining figures in Maiden's Forest Flora illustration (Pl. 163, figs. A-M) are from Braidwood district specimens and are quite distinct from *T. oreades*. *T. oreades* is stated by Mueller to be arborescent, and by Baker (1919) to be "a fair sized tree" producing "one of our most beautiful Australian ornamental timbers". Maiden (1911) states: "It has a diameter of 1½ up to 2 feet, and a height of 30 to 40 feet (Baeuerlen)". The Braidwood specimens, on the other hand, are shrubby plants, 3-7 feet high with slender branches. They are here designated:

*TELOPEA MONGAENSIS*, n. sp.

"Monga Waratah."

Frutex ramis gracilibus 1.0-2.3 m. longis; ramorum apices juveniles plus minusque lenticellati, paullo pubescentes. Folia glabra, lanceolata, integra vel apicibus 2-3-sinuosa, 7.5-10.0 cm. longa, 1-2 cm. lata, subtus pallida venulis quam in *T. oreades* et *T. speciosissima* tenuiovibus flores in racemis brevibus, latis, densis, planis, vel non convexis ut in *T. speciosissima*, glabris. Involucri bracteae coccineae, 1-2 cm. longae, mucronatae, glabrae praeter in marginibus tenuiter rubiginoso-ciliatis. Flosculae geminatae bracteolis circa 1 cm. longis praeditae. Folliculi 5.0-7.5 cm. longi stylo incluso.

Species ante id tempus cum *T. oreades* F.v.M. confusa.

Plants of a shrubby habit with slender whip-stick-like branches stringing from the root-stock and varying in length from 1.0-2.3 metres. Young or juvenile growth of the upper part of the branches slightly pubescent and more or less pitted with minute lenticels. Leaves glabrous, lanceolate, entire or with 2 or 3 sinuate lobes at the apex, especially in the juvenile stage, 7.5-10.0 cm. long, 1-2 cm. broad, slightly paler on the underside, the venation less conspicuous than in *T. oreades* and *T. speciosissima*. Flowers arranged in short, broad, compact racemes, flat or not domed as in *T. specio-*

*sissima*, glabrous, surrounded by crimson involucre bracts 1-2 cm. long, distinctly mucronate, glabrous except on the margins which are sparsely fringed with rusty-coloured hairs. Florets in pairs, supported by smaller bracteoles, about 1.0-1.5 cm. long. Fruit a follicle 5.0-7.5 cm. long from stipe to end of style.



Fig. 1.—*Telopea mongaensis*, n. sp. A, Flowering twig; B, Bud; C, Bud more advanced; D and E, Front and back view of opened flower; F, Side view of same; G, Pistil showing: a, Stipitate ovary; b, Style; c, Stigma; d, Hypogynous gland; e, Pedicel; H, Anther; K, Follicle; N, Sinuate-lobed leaf. (All approximately half natural size.)

*Holotype*: Sugar-loaf Mountain, near Braidwood, J. L. Boorman, x.1915, No. 1842 in the National Herbarium of New South Wales.

Having visited Monga, near Braidwood, in October, 1932, I was fortunate in gathering seeds of the Monga plants which were cultivated at Ashfield. It was noted that the early stage of growth developed entire lanceolar-shaped leaves, and the upper leaves were 2- to 3-sinuately-lobed. Unfortunately the plants did not survive. It is interesting to note that Maiden (1911, p. 70) also states: "Attempts to cultivate it in the Sydney district have been a failure so far."

A note by Boorman on the holotype sheet, dated 6.xii.1915, reads: "Frutescent plants of 4-8 ft. high, much branches and forming close compact growing small shrubs,

popularly known locally as 'the Waratah.'" The specimen is illustrated in Fig. 1, prepared by Mr. Guyot, who has superimposed on the foliage of the type a flower head from another specimen: Monga, W. Baeuerlen, xi.1899, No. 1843 in the National Herbarium of New South Wales, that of the type being deficient.

Other specimens examined in the same Herbarium, all previously determined as *T. oreades*, but now identified as *T. mongaensis*, are as follows: Mountains east of Braidwood, E. Betche, xii.1891, No. 1850; Clyde Mt., near Braidwood, J. L. Boorman, i.1915, No. 1849; Currockbilly, J. L. Boorman, ii.1910, No. 1848; Monga or Sugar-loaf Mt., near Braidwood, J. L. Boorman, iii.1909, No. 1847; Charlie's Forest, near Braidwood, J. L. Boorman, ix.1915, No. 1846; Charlie's Forest, near Braidwood, J. L. Boorman, iii.1909, No. 1845; Monga, W. Baeuerlen, xi.1884, No. 1844.

#### ACKNOWLEDGEMENTS.

I desire to express my thanks to Mr. R. H. Anderson, Chief Botanist and Curator, Botanic Gardens, Sydney, for help and for the use of Herbarium specimens; also to Mr. A. L. Guyot for preparation of the illustration.

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## STUDIES ON AUSTRALIAN MARINE ALGAE. III.

GEOGRAPHICAL RECORDS OF VARIOUS SPECIES AND OBSERVATIONS ON ACROCHAETIUM BOTRYOCARPUM (HARV.) J. AG. AND PTEROCLADIA CAPILLACEA (GMEL.) BORN. AND THUR.

By VALERIE MAY, M.Sc. (C.S.I.R., Marine Biological Laboratory, Cronulla, N.S.W.\*)

(Plate xix.)

[Read 27th November, 1946.]

## GEOGRAPHICAL RECORDS.

Part ii of this series of studies (May, 1946) records the occurrence in Australia of certain algae and extends the known range here of other species. Similar observations on other species are recorded below. The specimens quoted are located either in my own herbarium (quoted as VM) or in the National Herbarium of New South Wales (quoted as NSW).

## MELANOPHYCEAE.

## PETROSPONGIUM RUGOSUM (Okamura) S. &amp; G.

*New Record for Australia.*

This identification is based on the description and illustration given by Setchell and Gardner (1925). This species is known previously from both Japan and California, U.S.A., but the present is the first record of the genus occurring in Australia. Here, as elsewhere, *Petrospongium rugosum* occurs in the littoral zone, adhering to rocks which are exposed to surf between tides.

The zoosporangia are described by Setchell and Gardner (p. 509) as "attached laterally a little below the middle"; their illustration (Plate 39, fig. 42) shows this mode of attachment in mature zoosporangia, while in young stages the attachment is shown as basal. In the Australian material examined, full-size zoosporangia are attached either basally or laterally.

Locality.	Date.	Herbarium.	Notes.
Newport, near Sydney, N.S.W. . . . .	x.1944.	VM No. 429.	
Long Reef, near Sydney, N.S.W. . . . .	x.1944.	VM No. 162.	
Long Reef, near Sydney, N.S.W. . . . .	xi.1944.	VM No. 430.	
Bilgola, near Sydney, N.S.W. . . . .	xi.1945.	VM Nos. 921, 922.	
Malabar, near Sydney, N.S.W. . . . .	vii.1945.	VM No. 843.	
Coogee, near Sydney, N.S.W. . . . .	x.1914.	NSW	Collected by A. H. S. Lucas, previously labelled <i>Peyssonnelia</i> sp.

## PACHYDICTYON PANICULATUM J. Ag.

*New Record for New South Wales.*

This species is known from the southern coast of Australia, but the present are the first records of it from New South Wales.

Locality.	Date.	Herbarium.
Moruya, S. Head Beach . . . . .	7.i.1943.	VM No. 985.
Warden's Head, Ulladulla . . . . .	13.i.1946.	VM No. 2040.

\* Contribution No. 60 from the Laboratory.

## SPATHOGLOSSUM CORNIGERUM J. Ag.

*New Record for Queensland.*

This species is known from New South Wales as far north as Port Stephens, and is now recorded from Queensland.

Locality.	Date.	Herbarium.	Notes.
Margate, Moreton Bay, Qd. . . . .	xii.1943.	VM No. 984.	Drift.

## DICTYOPTERIS PARDALIS (Harv.), n. comb.

*New Record for Eastern Australia.*

This species was described (Harvey, 1855, p. 535), figured (Harvey, 1863, Pl. 29) and distributed (Harvey's Alg. Aust. Exsicc., No. 86) as *Haliseris pardalis*. Setchell and Gardner (1925, p. 656) give reason for the adoption of the generic name *Neurocarpus* Web. and Mohr. in preference to the name *Haliseris* Targ.-Tozz. ex Ag., and this is the procedure I have adopted previously with this genus. However, the latest Congress on International Rules has again listed *Dictyopteris* as "nomina conservanda proposita" in preference to *Neurocarpus*, so that I now adopt this generic name and *H. pardalis* now becomes *D. pardalis*.

Previously *D. pardalis* was known only from Western Australia (Geraldton to Broome); the present record from Queensland suggests that this species may occur along the north Australian coast, of which the algae have been as yet but little examined.

Lucas (1935) compared *H. pardalis* with *H. crassinervia* Zan. from Lord Howe Island. The two species appear to be very alike, and they may yet prove to be the same.

Locality.	Date.	Herbarium.	Notes.
Margate, Moreton Bay, Qd. . . . .	xii.1943.	VM No. 991.	Drift.

## RHODOPHYCEAE.

## BANGIA FUSCOPURPUREA (Dillw.) Lyngb.

*New Record for New South Wales.*

The identification of this species is based upon comparison with the illustration and description given by Okamura (1921). *B. fuscopurpurea* is known in the Pacific from California, U.S.A., as well as Japan, but the present appears to be the first record of it from Australia other than a passing reference by Laing (1928). It seems that in Australia this species has previously been recorded as *B. atropurpurea* viz., by Lucas, who recorded that species from Tasmania (1913) and New South Wales (1914). *B. fuscopurpurea* appears to be the salt-water counterpart of the fresh-water *B. atropurpurea*. Local New South Wales records definitely refer to marine algae, and the Tasmanian location given (Blackman's Bay, Derwent River) is almost certainly a salt-water collection, too. I have examined Lucas' material (Herb. NSW) and see no difference whereby it could be distinguished from *B. fuscopurpurea*. Thus his records appear to refer to *Bangia fuscopurpurea*, and are cited below as such, together with additional collections made by the writer.

Locality.	Date.	Herbarium.	Notes.
R. Derwent, Tasm. . . . .	vi.1909.	NSW	Collected by L. Rodway.
R. Derwent, Tasm. . . . .	viii.1909.	NSW	Collected Estuary by L. Rodway.
Bondi, near Sydney, N.S.W. . . . .	iii.1910.	NSW	Collected by A. H. S. Lucas.
Coogee, near Sydney, N.S.W. . . . .	x.1914.	NSW	Collected by A. H. S. Lucas.
Wattamolla, near Sydney, N.S.W. . . . .	viii.1944.	VM No. 215.	In rock pools.
Collaroy, near Sydney, N.S.W. . . . .	x.1944.	VM No. 150.	On horizontal concrete above rock
Corrimal Headland, near Sydney, N.S.W. . . . .	iii.1945.	VM No. 647.	baths.

Locality.	Date.	Herbarium.	Notes.
Narrabeen Headland, near Sydney, N.S.W. . . . .	v.1945.	VM No. 745.	Far out rocks.
Curl Curl, near Sydney, N.S.W. . .	xii.1945.	VM No. 1161.	On dry rock low-tide level.
Narrabeen Lake, near Sydney, N.S.W.	vii.1946.	VM No. 2098.	Riptide region.
Kiama, N.S.W. . . . .	vi.1945.	VM No. 821.	On far out rock exposed at low tide.

## CHAMPIA COMPRESSA HARV.

*New Record for New South Wales.*

This species was originally described from South African material, and was later recorded by Harvey (1863) as occurring in Australia, both in Western Australia and Victoria.

Material from New South Wales now referred to *C. compressa* appears to agree with Harvey's description and illustration (1847, p. 78, Pl. 30) and occurs in small quantities with moderate frequency on headlands in rock pools exposed at low tide. The growing plant is vivid blue and iridescent and so is easily located.

*C. compressa* resembles *C. Laingii* Lind. from New Zealand, since it has a compressed and iridescent thallus. The New Zealand species, however, is larger and more dorsal-ventral than the Australian one.

Locality.	Date.	Herbarium.	Notes.
Mona Vale, near Sydney, N.S.W. . .	11.iii.1945.	VM No. 523.	Tetrasporic.
Malabar, near Sydney, N.S.W. . . .	7.vii.1945.	VM No. 845.	
Mona Vale, near Sydney, N.S.W. . .	29.iii.1946.	VM No. 2047.	Tetrasporic.
Mona Vale, near Sydney, N.S.W. . .	29.iii.1946.	VM No. 2048.	Cystocarpic.
Mona Vale, near Sydney, N.S.W. . .	29.iii.1946.	VM Nos. 2049-52.	
The Entrance, Lake Illawarra, N.S.W.	25.iii.1945.	VM No. 641.	Tetrasporic.
Green Island, Entrance to Lake Conjola, N.S.W. . . . .	3.v.1946.	VM No. 2068.	

## SPECIES EXCLUDENDAE.

*Bangia atropurpurea* (Roth) Ag. from Tasmania and New South Wales. Discussed above under *B. fuscopurpurea*.

## COLLECTIONS FROM NORTH-WEST AUSTRALIA.

The three species listed below were collected by G. P. Whitley while on the "Isobel" Fisheries Survey of north-west Australia. The marine flora of this area is very inadequately known, so that this small collection is therefore welcome and worthy of record.

## TURBINARIA ORNATA J. Ag.

Locality.	Date.	Herbarium.	Notes.
Long Island, near the Dampier Archipelago, W. Aust. . . . .	1.xi.1945.	VM No. 2085.	This specimen agrees with that illustrated in Turner (1808, p. 50, Pl. 24, figs. c-h). The species is known previously from north and north-east Australia, also from Ceylon, the Andaman Islands, etc.

## CYSTOPHYLLUM prob. MURICATUM (Turn.) J. Ag.

Locality.	Date.	Herbarium.	Notes.
Long Island, near the Dampier Archipelago, W. Aust. . . . .	1.xi.1945.	VM No. 2086.	Very small scraps (with vesicles) were included with the above quoted <i>Turbinaria</i> collection. This species occurs in estuarine waters of most of Australia.

## NODULARIA prob. SPUMIGENA Mert.

Locality.	Date.	Herbarium.	Notes.
Floating 25 m. east of Bedout I., W. Aust. . . . .	23.x.1945.	VM No. 2087.	This genus occurs widely in ocean surface collections.

## OBSERVATIONS ON ACROCHAETIUM BOTRYOCARPUM (Harv.) J. Ag.

Papenfuss (1945) recently reviewed the *Acrochaetium-Rhodochorton* complex; on page 313 of this work he discusses *A. botryocarpum*, and queries the accuracy of Harvey's report that tetraspores are produced in this species. In order to check this detail the present writer examined Harvey's Alg. Aust. Exsicc. No. 523 labelled *Callithamnion botryocarpum*, from King George's Sound, Western Australia (Herb. NSW). This specimen shows monospores copiously developed in clusters, but there are no tetraspores. Harvey's material thus agrees with that illustrated by Hamel (1928, fig. 42), and the present finding supports Papenfuss' and Hamel's contention that Harvey's description in this case was inaccurate. These observations eliminate the only probable instance of an alternation of generations among the known species of *Acrochaetium*.

## CYSTOCARPS OF PTEROCLADIA CAPILLACEA (Gmel.) Born. and Thur.

In Australian collections of *Pterocladia capillacea* there appears to have been a remarkable absence of cystocarpic material.

A. H. S. Lucas worked for many years on Australian algae and reported (quoted by A. and E. S. Gepp, 1906): "I have never been able to get cystocarps, though I have examined great numbers of specimens at all seasons." A. and E. S. Gepp (1906) record further that a specimen collected by J. Bracebridge Wilson at Port Phillip Heads (Victoria) in 1890 was likely to be "the only fruiting specimen from Australia".

The present writer, however, has found cystocarpic material in moderate abundance. These cystocarpic plants were growing in near proximity to others which were either sterile or which bore tetraspores. On each occasion, however, the plants bearing cystocarps were growing in regions very much more shaded than those occupied by other specimens of the species. Thus the occurrence of cystocarp-bearing plants of the species appears to be dependent on ecological factors.

Plate xix, figure 1, shows a shaded rock pool in which cystocarpic plants were growing under the rock ledge indicated. Plate xix, figure 2, shows large areas of sterile specimens growing in exposed sunny areas. This latter is the more usual habitat for the species.

Collections of cystocarpic plants of *Pterocladia capillacea* are listed below.

Locality.	Date.	Herbarium.
Stanwell Park, N.S.W. . . . .	26.iii.1945.	VM No. 652.
Fairy Bower, near Sydney, N.S.W.	28.iv.1945.	VM No. 700.
Northern Head, Manly, near Sydney, N.S.W. . . . .	5.v.1945.	VM Nos. 737,
Careel Head, Whale Beach, near Sydney, N.S.W. . . . .	1.i.1946.	739. VM No. 1190.

## SUMMARY.

*Petrospongium rugosum* is recorded for the first time from Australia. The occurrence is recorded for the first time of three algal species from New South Wales, one from eastern Australia and another from Queensland. A small collection of algae from north-west Australia is recorded.

*Bangia atropurpurea* is excluded from the list of marine algae of Australia.

Observations on *Acrochaetium botryocarpum* show the presence of monospores, not tetraspores, as had been originally recorded.

The occurrence of cystocarpic plants of *Pterocladia capillacea* in Australia is shown to be dependent on ecological factors.

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## EXPLANATION OF PLATE XIX.

Fig. 1.—Shaded rock pool in which cystocarpic plants of *Pterocladia capillacea* were growing.

Fig. 2.—*Pterocladia capillacea* growing in its usual habitat on exposed rocks near low-tide level.

A REVIEW OF THE SPECIES *CALADENIA CARNEA* R.Br. (ORCHIDACEAE).

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

[Read 25th September, 1946.]

This variable terrestrial orchid occurs in all Australian States except Western Australia, where its record is very doubtful. Mr. C. A. Gardner, Government Botanist, Perth, writes: "I can find no specific reference to it by Rogers, although when I submitted the list of the Orchidaceae for my 'Enumeratio' to him, he left this species in as Western Australian. It is not in the Goadby Collection, nor is it in the Perth Herbarium. If you cannot find any published account of its occurrence here (apart from mine and Mrs. Pelloe's), I think that I would delete it from the Western Australian flora."

It extends (in the form of two small varieties) to New Zealand, is of doubtful occurrence in New Caledonia, and according to a personal communication from the late Dr. Rogers, *C. carnea* var. *gigantea* is found as far north as Java.

In the present writer's opinion, it is inadvisable to include in this species any form which entirely lacks the characteristic *transverse red striae* on the labellum and/or column. It is one of the most variable of all our terrestrial orchids; but in all the forms which I recognize as mere variants, this transverse striation is a constant feature, except in rare isolated specimens which are obviously abnormal. It is clear, then, that I cannot accept *C. carnea* var. *aurantiaca* Rogers (*Trans. Roy. Soc. S. Aust.*, xlvi, 1922, 154); and later in this paper will be found my reasons for raising this variety to specific rank.

It is desirable here to discuss the synonymy of *C. carnea* as given by Bentham (*Fl. Aust.*, vi, 386). In my "Orchids of New South Wales", 1943, 63, I followed Bentham in accepting *Arethusa catenata* Sm. (*Caladenia catenata* (Sm.) Druce, *Rep. Bot. Exch. Cl. Brit. Is.*, 1916, 611) as a synonym. But a subsequent study of Smith's plate and description (in the Mitchell Library at Sydney, *Exot. Bot.*, ii, 1804, 89, t. 104), has altered my opinion on the matter. The colouring of the flower in Smith's plate (mauve shading to deep purple, with a *blue labellum*) is nowhere else on record as occurring in *C. carnea*, but although colour is not to be ignored, great importance cannot be attached to it in a variable species. However, in addition to colour, the following distinctive points about Smith's flower preclude its acceptance as a representation of *C. carnea*:

- (1). The perianth is conspicuously dotted with dark spots.
- (2). The labellum is not lobed.
- (3). The margins of the labellum are entire.
- (4). The calli of the disc are shown prostrate and overlapping, in two chain-like rows (hence, perhaps, the name *catenata*).
- (5). At the base of the labellum are 4 tall calli similar to those of *C. tutelata* Rogers.
- (6). No transverse striae on either column or labellum.

What, then, is *C. catenata* (Sm.) Druce? Except for the narrow-linear leaf it could be taken as a slightly inaccurate representation of *C. tutelata* Rogers. I certainly think it should be deleted as a synonym of *C. carnea* R.Br.

As further synonyms of *C. carnea*, Bentham cites *C. alata* R.Br. and *C. angustata* Hook. f. The reference in both cases to Hooker's *Fl. Tasm.*, ii, t. 125, leads to the conclusion that both must be ruled out as synonyms of the present species. In the first place, Lindley—not Hooker—was the author of the name *C. angustata*; and

*C. angustata* Lindl. is a perfectly valid species (see W. H. Nicholls, *Vict. Nat.*, xlvii, 1931, 158). Next, there is definitely something erroneous in Hooker's plate. The figure over the name *C. alata* is an excellent representation of *C. angustata* Lindl., while that above the latter name does not depict Lindley's species. Whether it correctly represents Brown's *C. alata* I cannot say, since no authentic specimens bearing this name are available in Australia. But in a personal communication to me, W. H. Nicholls suggested its identity with the plant then known as *C. alpina* Rogers; and with this suggestion I agree. Recently, however, it has transpired that *C. alpina* Rogers is identical with *C. Lyallii* Hook. f., formerly supposed to be endemic in New Zealand (see these PROCEEDINGS, lxx, 1945, 57, footnote). Since neither *C. Lyallii* nor *C. angustata* can be included in *C. carnea*, Bentham's synonyms of the latter must be dropped.

Bentham recognized two named varieties of *C. carnea*—*C. carnea* var. *alba* and *C. carnea* var. *quadriseriata*. Neither of these can stand. The former is Brown's *C. alba*; the latter is Lindley's *C. angustata*. The fact that, in the case of this species, neither Bentham's synonyms nor his varieties can be accepted in no way casts any reflection upon the great botanist himself: it merely illustrates the difficulty in dealing with a variable species from dried material of plants which have never been seen alive.

It is unnecessary here to enter into any detailed account of the distinguishing features which warrant specific separation between *C. carnea*, *C. alba* and *C. angustata*, as this has been adequately provided by Nicholls in the "Review of Certain Species of *Caladenia*" cited above for *C. angustata*. Although now requiring certain amendments and additions, the whole of this illustrated review, covering about 17 species, is of great value for reference purposes (*Vict. Nat.*, xlvii, 1931, 155–161 and 179–183).

Bentham's description of *C. carnea* (l.c., 386) may be taken as providing all the salient features of the typical form, which is widely and abundantly distributed from about the latitude of Proserpine in Queensland, southward through New South Wales, Victoria, South Australia and Tasmania. The colour of the flowers varies from palest pink to bright rose. In some areas whitish flowers are quite common, but the white is never as pure as in *C. alba*. Sometimes the flowers are sweetly scented, sometimes they are quite scentless. In numbers they range from one to as many as six. The glandular calli on the labellum, both discal and marginal, are club-headed, the "clubs" usually being yellow.

So far as I can ascertain, eight named varieties have been described and published, in addition to Bentham's two excluded above:

1. *C. carnea* var. *gigantea* Rogers, *Trans. Roy. Soc. S. Aust.*, li, 1927, 13.
2. " " " *pygmaea* Rogers, l.c.
3. " " " *aurantiaca* Rogers, l.c., xlvi, 1922, 154.
4. " " " *minor* (Hook, f.) Hatch, *Trans. Roy. Soc. N.Z.*, lxxv (3), 1945, 367.
5. " " " *exigua* (Cheesmn.) Rupp, these PROCEEDINGS, lxxix, 1944, 74–5.
6. " " " *gracillima* Rupp, *Qd. Nat.*, xi (4), 1940, 86.
7. " " " *ornata* Nicholls, *Vict. Nat.*, lxxii, 1945, 61, 63.
8. " " " *subulata* Nicholls, l.c.

Of these, I am unable to accept *C. carnea* var. *aurantiaca* Rogers as a true variety of *C. carnea*, and I propose here to raise it to specific rank—*C. aurantiaca*. My reasons for this proposal are as follows:

- (1). Both column and labellum are entirely devoid of transverse striae.
- (2). The column is about half as broad again as in any form of *C. carnea* known to me.
- (3). The labellum is practically lobeless.
- (4). There are no marginal calli on the labellum unless we can so call the irregularities of the margin near the apex; if we can, they are quite different from those of *C. carnea*.
- (5). Except for the small area of orange on the labellum, the flowers are as pure white as those of *C. alba*.

These distinctions seem to me quite as important as those which separate *C. carnea* from *C. alba*. *C. aurantiaca* is best known in Victoria; but some years ago I found it in abundance along the shores of the Myall Lakes, near Bungwahl, New South Wales, about 70 miles north of Newcastle, and it was collected by Mr. D. Cross at Calga, near Gosford, New South Wales, in September, 1945. At first, I had taken it to be a diminutive form of *C. alba* R.Br., and I am still disposed to think it closer to that species than to *C. carnea*; but a reference to Nicholls's plate (*Vict. Nat.*, xlvii, 1931, 160, Figs. v and vi) will show that here also there are important differences. The mid-lobe of the labellum as depicted by Nicholls does not quite agree with the original description by Rogers (l.c.); but some of the Bungwahl-Gosford specimens correspond with Nicholls's drawing precisely. A fuller description than has hitherto been given follows:

CALADENIA AURANTIACA, n. stat.

A small and very slender plant from 12 to 17 cm. high, with a very narrow-linear leaf rather more than half as long as the stem. Flower usually solitary, but occasionally two, the second on a filiform pedicel. Perianth segments white inside, conspicuously striped with green on the outside. Labellum pure white except the tip and the calli, which are deep, or sometimes bright, orange: entire or occasionally with obscure tendencies towards lobation, but never really lobed. Margins entire, or denticulate near the tip, the teeth irregular. Calli in two rows, with relatively large clavate heads and slender stalks. Column broader than in either *C. alba* or *C. carnea*, the wings also wider. No transverse striation on either labellum or column. Eastern Victoria and central to northern coastal districts of New South Wales.

The following notes are offered concerning the other seven varieties listed above.

1. *C. CARNEA* var. *GIGANTEA*.—The type form of this came from Bungwahl, New South Wales. However, it is widely distributed, having been recorded as far south as Airey's Inlet in Victoria (Nicholls). Northward it extends well into tropical Queensland, and Rogers expressed the opinion that it was identical with a Javanese form determined as *C. carnea*. It is a comparatively robust plant, seldom bearing more than two flowers; these range up to 5 cm. in diameter, and are usually bright rose-pink, with a strong musky perfume. The height ranges from about 18 to over 50 cm.

2. *C. CARNEA* var. *PYGMAEA*.—This form is in great contrast to the preceding, rarely exceeding 12 cm. in height. Plants often grow in clusters, especially on damp soil. The flower is usually solitary, very small, with deep reddish tints, especially on the under surface of the perianth segments. It is found chiefly in Victoria and Tasmania, but I have seen it once or twice in New South Wales.

3. *C. CARNEA* var. *MINOR*.—This is *Caladenia minor* Hook. f. (*Fl. Nov. Zel.*, i, 1853, 247). It is impossible to find any features distinguishing this plant from *C. carnea*. At one time I regarded it as scarcely differing from *C. carnea* var. *pygmaea*, and I included it in that form in these PROCEEDINGS, lxi, 1944, 74-5. But further material provided by E. D. Hatch of Auckland proved this a mistake; and Hatch has now published it as *C. carnea* var. *minor* (*Trans. Roy. Soc. N.Z.*, lxxv (3), 1945, 367). I have seen Australian specimens identical in all respects with those from New Zealand.

4. *C. CARNEA* var. *EXIGUA*.—Cheeseman first published this (*Trans. N.Z. Inst.*, xlv, 1913, 96) as a variety of *C. minor* Hook f. Subsequently (*Man. N.Z. Fl.*, 1925 ed.) he raised it to specific rank. It is, however, only a very diminutive form of *C. carnea*: structurally the only distinction I can find is the reduction of the marginal calli of the labellum to one on each side. I have collected this form at Longley in Tasmania and near the Hawkesbury River in New South Wales. It does not grow in clusters like *C. carnea* var. *pygmaea*, and the flowers are light pink.

5. *C. CARNEA* var. *GRACILLIMA*.—This very attractive form was found by the Rev. E. N. McKie near Yandina in southern Queensland. It is extremely slender, the flowers being bright pink, with narrow, almost acuminate sepals and petals. It is plentiful in the type locality, but I have not seen specimens from elsewhere.

6. *C. CARNEA* var. *ORNATA*.—A form from the Portland area in western Victoria, and perhaps the most beautiful member of the species. The labellum is brilliant red, traversed by darker striae across the broad lateral lobes. Very often the lateral sepals



are united from the base for about a third of their length. Nicholls states that the calli are occasionally gammate in shape, as in the Tasmanian *C. Longii* Rogers.

7. *C. CARNEA* var. *SUBULATA*.—This has some features in common with *C. carnea* var. *gracillima*; but the lateral sepals are conspicuously reflexed—a most unusual occurrence in this species; and the margins of the mid-lobe of the labellum are entire. It comes from the same area as *C. carnea* var. *ornata*.

In districts where both *C. carnea* and *C. alba* are plentiful, occasionally plants are found combining the characters of both, and therefore suggestive of natural hybridization. It is, however, rather surprising, in view of the close affinities between these two, that such cases are rare in proportion to the vast numbers of the plants. Near the Paterson River, in New South Wales, I found numerous specimens suggestive of *C. carnea* × *C. caerulea*. The flowers were solitary, pink, but with the labellum shaped like that of *C. caerulea*, to which further resemblance was manifested in the broad-linear, semi-prostrate leaf.

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TAXONOMIC NOTES ON THE GENUS *ABLEPHARUS* (SAURIA: SCINCIDAE).

## I. A NEW SPECIES FROM THE DARLING RIVER.

By STEPHEN J. COPLAND, B.Sc.

(Plate xviii; three Text-figures.)

[Read 27th November, 1946.]

## INTRODUCTION.

This paper—the first of a series in which I hope to discuss all Australian members of the Scincid genus *Ablepharus* Fitzinger—deals with an apparently new species from western New South Wales.

*ABLEPHARUS KINGHORNII*, n. sp.

*Diagnosis*: An *Ablepharus* with the frontoparietal single and interparietal distinct; differing from the only other Australian pentadactyl member of this group, *Ablepharus ornatus* Broom (1896, p. 343; Broom, R. On Two New Species of *Ablepharus* from North Queensland. *Ann. Mag. Nat. Hist.*, (6) 18: 106) from Muldiva, north Queensland, in having 22 midbody scale rows (*A. ornatus* 26–28), four supraoculars (*A. ornatus* 3), shorter limbs, colour, and other characters as given in Table 2.

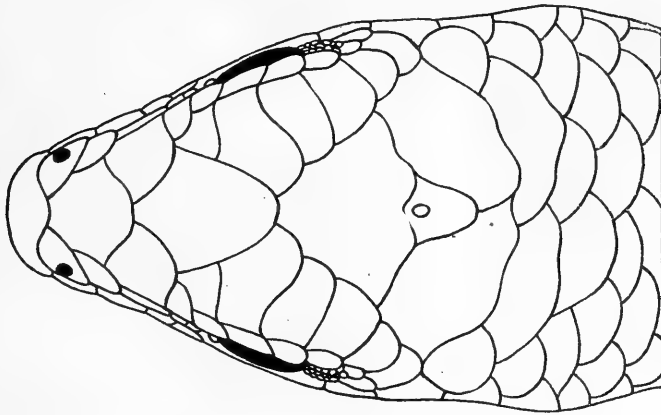
*Holotype*. No. R6458A in the Australian Museum; Darling River, between Bourke (30.5° S., 145.58° E.) and Wilcannia (31.28° S., 143.13° E.), New South Wales, collector Robt. Helms, May–June, 1890, “Darling River floods”.



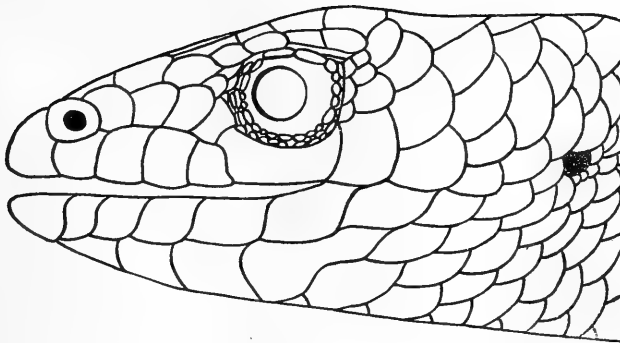
Fig. 1.—Map of New South Wales showing type locality of *Ablepharus kinghorni*, n. sp., “Darling River, between Bourke and Wilcannia”.

*Description of Holotype*.—Rostral not projecting; smoothly rounded when seen from above, the area visible being equal to about two-thirds that of the frontonasal; long, mainly concave but slightly sinuous, sutures with the nasals; concave sutures, about one-half the length of those with the nasals, with 1st supralabials; the short, convex junction with the frontonasal is equal to about one-fifth the width of the frontal. Nasals moderate, not in contact, roughly triangular; all sutures convex, long posterior one with

frontonasal and postnasal, slightly shorter anterior one with rostral, and still shorter one with 1st supralabial; well separated from 2nd supralabial; scale ungrooved except for slight vertical indentation behind nostril on left side; rounded nostril, with diameter equal to one-third length of scale, near ventral border. No supranasals. Postnasal subequal in size to nasal; long, sweepingly convex, dorsal and posterior border against frontonasal, prefrontal, and anterior loreal; mainly concave but slightly irregular suture with nasal; short, nearly horizontal one with 2nd supralabial; and quite short straight one with 1st supralabial. Frontonasal large, equal to at least two-thirds the area of the frontal, with which it forms a suture about one-tenth or less the width of the latter scale; long, very slightly concave sutures with prefrontals, and considerably shorter, both subequal in length, with the postnasal and nasal; that with the rostral being shorter again. Prefrontals large, nearly equal to one-half the area of the frontal, roughly quadrilateral; two long, nearly straight sides against frontal and frontonasal; shorter, slightly concave ones against postnasal and 1st supraciliary, considerably shorter with anterior loreal, while it meets the 1st supraocular at little more than a point. Frontal large, kite-shaped though rather squat, width equal to that of the supraocular region at its widest, length equal to its distance from the tip of the snout; very narrowly in contact anteriorly and posteriorly with the frontonasal and frontoparietal respectively; sides against prefrontals, 1st and 2nd supraoculars; just separated from 1st supraciliaries. Frontoparietal single, equal in length to the frontal, but considerably wider and larger; long, sinuous sutures with parietals; on each side the contacts with 2nd, 3rd and 4th supra-



2



3

Figs. 2-3.—Head scales of *Ablepharus kinghorni*, n. sp. 2. Dorsal view. 3. Lateral view. Length of head, 7 mm.

oculars are subequal in length; indented against small kite-shaped interparietal. Interparietal rounded behind, enclosed between parietals, somewhat less than one-half the length of the frontoparietal; has a dark rounded pineal area in the anterior third. Parietals each nearly equal to the frontoparietal in size, irregularly oblong; long axes, which diverge at about 90°, twice the length of the short; meeting behind the interparietal in an oblique suture sloping backwards towards the right; other sutures, convex but irregular with nuchal; slightly shorter and straight with upper secondary temporal; about same length, sinuous, with frontoparietal; short with interparietal, 2nd postocular and 6th supraciliary, and very short with 4th supraocular. There is a single pair of nuchals, each twice the width of a following body scale. Seven supralabials, anterior four small; 2nd and 3rd, which are equal in size, squarish and slightly larger than 1st and 4th which are subequal and irregularly quadrilateral; 1st in contact anteriorly with rostral and dorsally with nasal and postnasal; 2nd dorsally with postnasal and anterior loreal; 3rd dorsally with posterior loreal and just touching anterior loreal and presubocular; 4th dorsally with presubocular and posteriorly with 5th supralabial; 5th very large, equal in size to three of the four anterior supralabials, boat-shaped, long and concave upper margin forming the entire lower border of the eye; 6th and 7th taller but somewhat smaller than 5th, pentagonal, roughly haystack-shaped, lower margins horizontal, anterior and posterior vertical, and the other two sides meeting in a point dorsally; two small postlabials are separated by two scales from the ear opening. Primary temporal squarish, two posterior borders against upper and lower secondary temporals and 7th supralabial, anterior two against 2nd and 3rd postoculars and 6th supralabial. The upper secondary temporal is slightly larger than the lower which is again slightly larger than the primary. Two tertiary temporals, which are considerably larger than the following body scales, lie directly behind the still larger secondary temporals. Body scales begin behind the nuchals, tertiary temporals and postlabials. The two loreals are rough squares subequal in size; the anterior lies between postnasal, prefrontal, 1st supraciliary, posterior loreal, and 2nd and 3rd supralabials; the posterior between anterior loreal, 1st supraciliary, one of three small preoculars, presubocular, and 3rd supralabial. The eye is surrounded by about 20 triangular or roughly oblong granules, two dorsal ones being larger than the others. Outside this inner ring of granules are two other irregular rings. These granules are much the same size, except for three or four posterior ones of the outer circle which are enlarged. The outer ring is bounded by the 2nd to 5th supraciliaries above, 5th supralabial below, three small preoculars and presubocular anteriorly, and by 6th supraciliary, 1st and 3rd postoculars, and 6th supralabial posteriorly. The three preoculars, a triangular anterior one and two irregular scales behind, are together about half the area of a loreal. The presubocular is square, equal in size to a loreal, and lies between the two lower preoculars, posterior loreal, and 3rd, 4th and 5th supralabials. The postoculars are three small scales, the anterior 1st squarish and about half the size of the squarish antero-ventral 3rd, which is less than half the size of the oblong 2nd; the 2nd is noticeably larger than the 6th supraciliary, and lies between it, parietal, upper secondary temporal, primary temporal, and 1st and 3rd postoculars. Of the six supraciliaries, the 6th is larger than the 1st, which is larger than the 2nd, the remaining three are smaller again, squarish, and lie against the 2nd, 3rd, and 4th supraoculars respectively; the 1st is triangular and lies between prefrontal, 1st supraocular, 2nd supraciliary, two preoculars, and the two loreals; it is just separated from the frontal; the 6th is twice as high as wide and lies between 4th supraocular, parietal, 1st and 2nd postoculars, an enlarged granule, and 5th supraciliary. There are four well-developed supraoculars, the 2nd largest, then the 3rd, 4th and 1st; the frontal is in contact with the 1st and 2nd, the frontoparietal with the 2nd, 3rd and 4th, and the parietal very narrowly with the 4th. The large mental and postmental are followed by three pairs of chin-shields, the 1st and 2nd pairs being each separated by a single scale and the 3rd pair by three scales; each of the 3rd chin-shields is strongly prolonged posteriorly against a 6th infralabial. Six, or possibly seven infralabials, in order of decreasing size, 5, 4, 3, 2, 6, 1, 7.

The ear opening is irregularly rounded, without denticulation, considerably smaller than the pupil of the eye, and three scales behind the last supralabial.

Scales are 22 at midbody, subequal. Caudal scales larger, especially the transverse, subcaudal row. Two strongly enlarged preanal scales. Scales from above vent to parietals, 63.

Body rather elongate, the distance between the end of the snout and the forelimb is contained about twice in the distance between axilla and groin. Limbs moderately developed, well separated when adpressed. Lamellar formula for fingers, 6, 9, 13, 13, 8. Lamellar formula for toes, 7, 12, 15, 17, 10. All lamellae are compressed and spinose; most tubercles on the palm and sole are also sharp.

Measurements of the holotype are given with those of the paratypes in Table 1.

TABLE 1.  
*Measurements of the Holotype and Paratypes of Ablepharus kinghorni, n. sp., in mm.*

Number.	R 6458A.	R 6458B.	R 6459A.	R 6459B.	R 6460A.	R 6460B.
Snout-vent .. .. .	45	39	38	39	38	33
Tail .. .. .	54	54	28+	64	6+	30+
Snout-ear .. .. .	8	7	7	7	7	6.5
Snout-forelimb .. .. .	13	12	12.5	13	12	11.5
Axilla-groin .. .. .	27	22	22	22	22	18
Head, length .. .. .	7	6	6.5	6.5	6	5.5
Head, width .. .. .	5	4.5	4.5	5	4.5	4
Body, width .. .. .	6	6	5	6	5	4
Forelimb, length .. .. .	9.5	9	9.5	9.5	9	8
Hindlimb, length .. .. .	13	12	12	12	11	10
Tail/Snout-vent .. .. .	1.20	1.38	—	1.64	—	—
Axilla-groin/Snout-forelimb ..	2.08	1.83	1.76	1.69	1.83	1.57

The specimen is much bleached, but the original ground colour was probably medium brown. Most prominent markings are 10 white streaks contained within 11 brown ones extending longitudinally from the head to the base of the tail, where they are reduced in number. The white and brown lines, one of the latter being mid-dorsal, are practically similar in width, the white occupying the central half of each scale and the brown the edges on each side. All dorsal lines are equally distinct. The lateral ones, though still sharply defined, are not so prominent. There are longitudinal lines along the limbs. The lines become confluent or die out at the base of the tail, and those continuing posteriorly appear to end about the length of the hind limb from the vent. The remainder of the tail seems to have been a uniform brown. The underside except for the tail is whitish to light brown. The supraoculars and temporals and other head scales behind them are heavily margined with dark brown.

The species is named for Mr. J. R. Kinghorn, of the Australian Museum, as a slight recognition of his services to Australian herpetology, and also as thanks for much personal help and advice.

*Variation in Paratypes.*—Five specimens, Nos. R6458B, R6459A, R6459B, R6460A and R6460B, in the Australian Museum, with same particulars as the holotype R6458A, are undoubtedly paratypes in the strictest sense.

Comparison of the series shows only insignificant differences. The length of the suture between rostral and frontonasal in R6459B is equal to one-fifth the width of the frontal as in the holotype, but is slightly wider in the other four cases. In R6458B and R6459B the nasal and 2nd supralabial meet at a point. Prefrontals and 1st supraoculars have slightly longer contacts in the five paratypes than in the holotype. The tertiary temporals are prominent in some specimens, indistinguishable from body scales in others. The 2nd to 5th supraciliaries are roughly subequal in size in all paratypes. In R6459B the chin-shields are separated by 1, 2, and 3 scales instead of 1, 1, and 3 as in all the others. Every lizard has 22 midbody scale rows. Tail/snout-vent and axilla-groin/snout-forelimb ratios differ considerably as shown in Table 1, but I cannot regard the differences as significant. Lamellae beneath the 4th toes are 17 (once), 18 (twice), and 19 (twice). Markings and colour (allowing for unexplained differential bleaching) are identical in all specimens. The pattern is best seen in R6460B, which is figured in Plate xviii, and R6459A.

The main points of difference between *Ablepharus kinghorni* and *A. ornatus* are set out in Table 2.

TABLE 2.

	<i>A. kinghorni.</i>	<i>A. ornatus.</i>
Midbody scale rows .. ..	22.	26-28.
Snout .. ..	Short and rounded.	Short and pointed.
Prefrontals .. ..	Separated.	In contact.
Frontal .. ..	In contact with 1st and 2nd supraoculars.	In contact with 1st supraciliary and 1st supraocular.
Supraoculars .. ..	4, 2nd largest, well separated.	3, 1st larger than the other two together, 1st on each side closely approach each other.
Supraciliaries .. ..	6, 6th largest.	6, 1st largest.
Interparietal .. ..	Much smaller than frontonasal.	About equal in size to frontonasal.
Labials in front of subocular ..	4.	3.
Limbs when adpressed .. ..	Do not meet.	Hindlimb reaches to wrist.
Ear opening .. ..	Small, roughly rounded.	Moderate, oblique, oval.
Colour .. ..	Ten prominent dorsal and lateral white longitudinal stripes contained within 11 brown ones, extending from head to at least base of tail.	"All the dorsal region light fawn-coloured, uniform or with few very small irregular dark spots . . . along the upper third of each lateral region passes a dark brown interrupted strip broken into small irregular squares by alternating fawn-coloured squares . . . along the middle lateral region passes a narrow light-coloured strip free from any spots . . . along the lower third of the lateral region is a regular series of irregular darkish spots or mottlings . . ."

## ACKNOWLEDGEMENTS.

I wish to acknowledge help and advice from Professor W. J. Dakin and Professor E. A. Briggs, of the University of Sydney; also Dr. A. B. Walkom, Mr. J. R. Kinghorn and Mr. W. A. Rainbow, of the Australian Museum. Mr. Kinghorn also kindly lent me specimens. I have to thank Miss A. G. Burns, of the Department of Zoology, University of Sydney, for the photographs.

## EXPLANATION OF PLATE XVIII.

Figs. 1-3. *Ablepharus kinghorni*, n. sp.

Fig. 1.—Dorsal view of holotype, No. R6458A; length of head and body, 45 mm.

Fig. 2.—Dorsal view of paratype, No. R6460B; length of head and body, 33 mm.

Fig. 3.—Lateral view of No. R6460B.

Photos.—Miss A. G. Burns.

## NOTES ON AUSTRALIAN ORCHIDS. V.\*

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

(Eleven Text-figures.)

[Read 27th November, 1946.]

I. A REVIEW OF THE GENUS *Calochilus* R.Br.

This genus was established by Robert Brown in 1810 (*Prodromus*, 320). Its affinities are obscure. Brown placed it at the end of his second Section of the Orchidaceae, immediately after *Neottia australis*—now known as *Spiranthes sinensis* (Pers.) Ames. The first genus in his next Section was *Microtis*. Bentham (*Fl. Aust.*, vi, 314) placed *Calochilus* between *Spiranthes* and *Thelymitra*; while F. M. Bailey (*Qd. Fl.*, v, 1585) put it between *Glossodia* and *Chiloglottis*. In Pfitzer's arrangement of the Orchidaceae, as given in Torre and Harms, *Genera Siphonogorum Enscripta* (1900–1907), it stands between *Acidanthus* and *Eriochilus*. Clearly, then, there has been much difference of opinion as to its rightful position. So far as the habit and general conformation of the plants are concerned, there is much in common between *Calochilus* and *Thelymitra*; immature plants may easily be confused. The flowers, however, differ widely in their morphology, although the anomalous *Calochilus imberbis* Rogers might perhaps be considered to constitute something like a link between the two genera.

Though it cannot be said to have any bearing on the position of *Calochilus*, it may not be out of place here to call attention to the curious superficial resemblance between the South African orchid *Disa lugens* Bolus and a *Calochilus*. The former is illustrated in Bolus's *Orchids of the Cape Peninsula* (1918 ed., t. 87), and at first glance, the resemblance is very striking. There is actually no close affinity; the "beard" in the flower of *D. lugens* is formed by numerous fine incisions along the margins of the labellum, while in a *Calochilus* flower it consists of densely-massed, metallic-lustrous hairs. Nevertheless the resemblance is remarkable enough to constrain one to ask why so similar a form of flower should be evolved by orchids only remotely related, and separated by 5,000 miles of ocean. No other species of *Disa* figured by Bolus shares in the likeness.

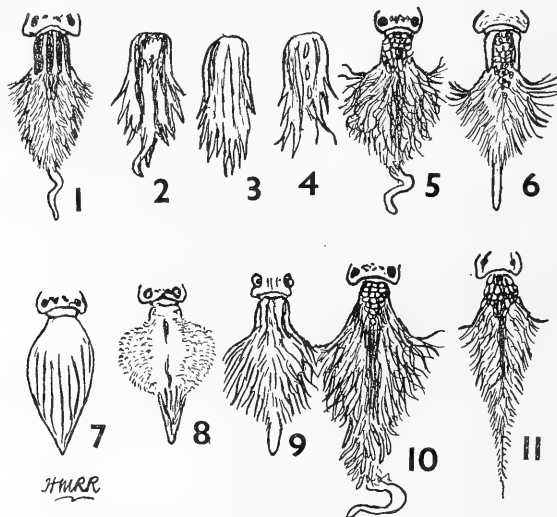
For many years *Calochilus* was believed to be endemic in Australia: but although apparently Australian in origin, it is now known to have at least one representative in New Caledonia (*C. neocaledonicus* Schltr.), and three or four in New Zealand—three of the known Australian species, and a fourth still under investigation. Robert Brown described only two species—*C. campestris* and *C. paludosus*. (References to the descriptions of species subsequently established will be found in the list following this paragraph.) Sixty-three years after the publication of Brown's *Prodromus*, Bentham added a third species, *C. Robertsonii*: and in 1892 F. Mueller described *C. Holtzei* from the Northern Territory. In 1918 R. S. Rogers published *C. capreus* as a new species; but subsequently this proved to be specifically identical with Brown's *C. campestris*. In 1927 the same author described a new Victorian species under the name *C. imberbis*, in allusion to the absence of the metallic-lustrous hairs so characteristic of the genus. This was followed two years later by another Victorian species, *C. Richae* Nicholls. In 1930 Rogers described *C. saprophyticus*, a remarkable form, the description of which was later amplified and illustrated by Nicholls. In 1934 Rupp described *C. grandiflorus*, which was followed nine years later by the same author's *C. gracillimus*.

\* Continued from these PROCEEDINGS, Vol. 69 (3-4), 1944, 73-75.

Including *C. neocaledonicus*, then, ten species are now recognized. The distribution of these, as far as it is at present known, is as follows:

1. *C. campestris* R.Br. All Australian States except Western Australia; also in New Zealand.
2. *C. paludosus* R.Br. Same range as No. 1.
3. *C. Robertsonii* Benth., *Fl. Aust.*, vi, 1873, 315. All Australian States and New Zealand.
4. *C. Holtzei* F. Muell., *Bot. Centr. Alb.*, 1, 1892, 127; and *Vict. Nat.*, viii, 1892, 80. Northern Territory.
5. *C. imberbis* Rogers, *Trans. Roy. Soc. S. Aust.*, li, 1927, 4. Victoria.
6. *C. Richae* Nicholls, *Vict. Nat.*, xlv, 1929, 233. Victoria.
7. *C. saprophyticus* Rogers, l.c., liv, 1930, 41; and Nicholls, l.c., lix, 1943, 158. Victoria; Tasmania? (see note below).
8. *C. grandiflorus* Rupp, *Vict. Nat.*, 1, 1934, 239. Southern Queensland and north coast of New South Wales.
9. *C. gracillimus* Rupp, l.c., lx, 1943, 28, and in *Orch. N.S.W.*, 1943, Plate vii. New South Wales.
10. *C. neocaledonicus* Schitr., Engler's *Bot. Jahrb.*, xxxix, 1907, 43. As this species is endemic in New Caledonia, it will not be referred to further. I have not seen a specimen.

1. *C. campestris*.—The plant figured by R. D. Fitzgerald over this name in *Aust. Orch.*, i, 4, is not Brown's species, but accurately represents the pale-flowered form of *C. Robertsonii* Benth. The finest illustration of *C. campestris* known to me is that in Curtis's *Bot. Mag.*, 1832, t. 3187. The plant there depicted was a Tasmanian specimen. In *Vict. Nat.*, lviii, 1941, 94, there is an excellent black-and-white plate by Nicholls in which he shows the curious variations of the labellum. After the publication of *C. cupreus* by Rogers in 1918, I was puzzled by finding that nearly all New South Wales specimens which came into my hands, supposedly as *C. campestris*, appeared to agree very closely with the new species. It looked almost as if Brown's species had disappeared. Later on I became convinced that these two really were not specifically distinct, confusion having been caused by the imperfectly known variations in *C. campestris*. I then learned that Nicholls had reached the same conclusion in Victoria, and was about to publish the result of his investigations.



Figs. 1-11.—Labella and column-bases of various species of *Calochilus*. 1. *C. campestris*. 2-4. Variations in the posterior portion of the labellum of *C. campestris*. 5. *C. Robertsonii*. 6. *C. paludosus*. (Note absence of columnar glands.) 7. *C. imberbis*. 8. *C. Richae*. 9. *C. saprophyticus*. 10. *C. grandiflorus*. 11. *C. gracillimus*. (2, 3, 4, 7, 8 and 9 partly after W. H. Nicholls.)



2. *C. paludosus*.—This is adequately figured by R. D. Fitzgerald, l.c., though certain details lend themselves to misapprehension (see my *Orch. N.S.W.*, 1943, note on p. 52). The specific name chosen by Brown is not particularly appropriate, for this plant is not specially addicted to swampy ground. The finest specimen I have ever seen—a plant 90 cm. high with 15 flowers—was collected by me in a dry scrub on the South Maitland coalfields. Apart from the brilliant red of the labellum hairs, *C. paludosus* may usually be readily distinguished from other species by the wide expansion of the petals and lateral sepals: the dorsal sepal is often conspicuously cucullate.

3. *C. Robertsonii*.—This is the only species which is known to extend to Western Australia. The colour of the metallic-lustrous hairs varies from peacock blue to purple or purplish-red, but occasionally plants are found with pale green or greenish-white flowers. This peculiarity is shared by *C. paludosus* and *C. grandiflorus*. Bentham named the species in honour of J. G. Robertson of Wando Vale, in western Victoria; but he invariably mis-spells "Wando" as "Wendu". Robertson was a Scot who emigrated to Tasmania in 1831, and for some years he was manager of the Formosa Estate there. He was a friend of Ronald Gunn, who collected so assiduously for J. D. Hooker during the preparations for his "Flora Tasmaniae". Robertson left for Victoria in 1840, and settled at Wando Vale near Casterton. Sharing his friend Gunn's enthusiasm for botany, he collected extensively along the Glenelg River and its affluent, the Wando, and also about Portland. When he finally returned to Scotland he gave his herbarium to Sir William Hooker at Kew, where Bentham had access to it.

4. *C. Holtzei*.—I have seen no specimen of this. As little appears to be known about it, I give here Baron von Mueller's description published in the *Victorian Naturalist*, March, 1892.

"Lower calyx-lobes ovate-lanceolar, a quarter of an inch long, upper one broader, verging into deltoid-roundish form; petals obliquely lanceolar-elliptical, fully as long as the calyx-lobes. Perianth light greenish-brown. Labellum twice as long as the other lobes, rhomboid-ovate, greenish, above densely beset and ciliolar-fringed with reddish hairs, but glabrous at the deltoid apex. Near the middle of the base, two straight vertical dark-blue plates with prominent striae between them, but devoid there of glandules or protruding cross-lines. Column as in other species. Height to three feet. Flowers to twenty."

This description appears to confuse the base of the labellum with that of the column; it is the latter, not the former, which would be "devoid of glandules or protruding cross-lines". Apparently the dark gland at the base of each side of the column, which is so conspicuous in most species, is absent in *C. Holtzei* as it is in *C. paludosus*. The unusual length of the petals, and the deltoid apex to the labellum, are other distinctive features.

5. *C. imberbis*.—This may truly be termed an anomalous member of the group, since it lacks the very *raison d'être* of the generic name, which alludes to the beautiful adornment of the labellum by its metallic-lustrous glandular hairs. The labellum of *C. imberbis* is quite glabrous. Rogers follows up his description of the species with the following remarks: "The flowers, though not so regular as in the genus *Thelymitra* Forst., show an approach to actinomorphy which is very unusual in orchids. The lip is distinctly petaloid; but the lateral petals retain the shape which is common to all known species of *Calochilus*."

The type locality is Rushworth, in the mid-north of Victoria. The discoverer of this peculiar species was Mrs. F. Rich, whose name is commemorated in the next species. Subsequently *C. imberbis* was found by Mrs. Edith Coleman at Ringwood, on the eastern outskirts of Melbourne.

6. *C. Richae*.—This was discovered by Mrs. Rich at Whroo, which may be considered as portion of the Rushworth area. It differs from the typical *Calochilus* almost as strikingly as *C. imberbis*; for the labellum, although not glabrous, is clothed with hairs so short as to constitute a mere pubescence. It is very differently shaped from that of *C. imberbis*, the pubescent portion being almost orbicular. Up to the present there is no record of the occurrence of *C. Richae* beyond the type locality, and it appears to be very rare, though found in sufficient numbers to warrant specific rank.

7. *C. saprophyticus*.—As indicated above, the original description by Rogers of this curious and interesting species has been amplified and illustrated by Nicholls (*Vict. Nat.*, lix, 1943, 158). If Nicholls's plate be compared with that in Hooker's *Flora Tasmaniae*, ii, t. 106A (over the name *C. campestris* R.Br.), I think the specific identity of the two plants will be found fairly obvious. Compare, again, this plate of Hooker's with that cited above (under *C. campestris*) from Curtis's *Botanical Magazine*. It can scarcely be maintained that they represent the same species. This explains why, in the records of distribution given above, I have credited *C. saprophyticus* with extension to Tasmania, but with a note of interrogation, since it has not been recorded there under that name. I believe that Hooker's plate does represent this species, and that it will be found again in Tasmania. Morphologically, it is close enough to *C. campestris* to be mistaken for a form of that species; but the stem is yellowish, and the leaf scarcely differs from the stem-bracts. The root-system resembles that of *Prasophyllum flavum* R.Br., the irregularly-shaped tubers being accompanied by several fleshy rhizomes. The species has been recorded from three widely-separated areas in Victoria—Cravensville (north-east), Angelsea (central-western), and Portland (extreme west).

8. *C. grandiflorus*.—Though not usually a robust plant, this species has the largest, and perhaps the most beautiful, flowers in the genus. The deep reddish-purple hairs massed on the lower half of the labellum are in very striking contrast to those on the anterior portion, which are translucent and sparkling with papillae. Whether *C. grandiflorus* is identical with the form which Bentham named *C. campestris* var. *grandiflora* (*sic*), is a question which could only be settled by comparing it with the specimens he cites; but it certainly cannot be included in *C. campestris*: its affinities are rather with *C. Robertsonii*. But it is sufficiently distinct from any other form to stand on its own merits as a species. It occurs along the coast of southern Queensland, extending inland as far as Stanthorpe; and also, sparingly, along the north coast of New South Wales, its southern limit apparently being about the Myall Lakes. It grows in bogs or swampy ground. The flowering period is from late October through November.

9. *C. gracillimus*.—This latest addition to the species of the genus is also the latest to flower, appearing about Christmas time. It is a very slender form in all its parts, and the labellum is exceptionally long. The reddish-purple hairs often extend nearly to the summit of the filiform tip of the labellum. The columnar glands are not united by a ridge or coloured band, and each has a short, dark venule entering it at the top and the bottom. *C. gracillimus* is recorded from Woy Woy, Gosford, and the Blue Mountains, all in New South Wales.

R. D. Fitzgerald was of the opinion that *C. campestris*, *C. paludosus*, and other forms known to him, were self-fertilized. As, however, he was mistaken in his interpretation of *C. campestris*, his remarks on that species really apply to *C. Robertsonii*. We now know that *C. campestris* R.Br. is pollinated by the agency of the flower-wasp *Campsomeris (Dielis) tasmaniensis*. The whole process was carefully watched by Mr. and Mrs. F. Fordham at Brunswick Heads in northern New South Wales, in September, 1945; and the results of their observations were published (*Vict. Nat.*, lxii, 1946, 199). Fordham's statements leave no room for doubt on the matter. Whether the species is entirely dependent on the wasp, or is sometimes self-fertilized, is another question. It is worth noting that Fordham says the wasps paid no attention whatever to flowers of *C. Robertsonii* which were mixed with those of *C. campestris* during the two days of observation. The hairs on the labellum of the former are more densely massed than in the latter species. If, however, the dense "beard" of a *Calochilus* labellum is intended to repel insects, why is it so brilliantly coloured? One would also like to know whether the two "beardless" species, *C. imberbis* and *C. Richae*, are self-fertilized, or by what insect agency pollination is effected.

## II. ACIANTHUS CAUDATUS R.Br. var. PALLIDUS, n. var.

Planta 7–10 cm. alta, cum floribus viridis aut flavoviridis. Flores plerumque 2. Sepalum dorsale erectum, 20 mm. longum, pilatum cuspidè filiforme; margines anteriores plicati. Sepala lateralia anguste linearia, patentia, 13 mm. longa. Petala linearia,

patentia vel deflexa, 5 mm. longa. Labellum rhombolanceolatum apice recurvo, calli basales truncati. Columna magnopere exserta.

Plant 7-10 cm. high, green or yellowish-green, including the flowers. Flowers usually 2. Dorsal sepal erect, 20 mm. long, spear-shaped with a filiform point, the margins plicate upwards. Lateral sepals narrow-linear, spreading, 13 mm. long. Petals linear, spreading or deflexed, 5 mm. long. Labellum rhomboid-lanceolate, with an acute recurved tip; the two basal calli blunt. Column bent forward almost at right angles.

Cronulla, New South Wales, viii.1926 (E. Nubling). Smithton, north-western Tasmania, x.1946 (the type: Miss Mary Atkinson).

This is an interesting form, of which I have recently been able to make a critical examination from living plants forwarded by Miss Atkinson. Mr. Nubling's specimen in my herbarium, collected at Cronulla twenty years previously, agrees with the Smithton plants in all respects. The typical *A. caudatus*, though variable in size, sometimes attains a height of 16 cm., and may bear as many as six flowers, which are deep purplish-red or purplish-brown: the dorsal sepal is often more than twice as long as in the new variety. In my opinion the latter is strongly suggestive of a natural cross between *A. caudatus* and *A. exsertus* R.Br. Three characteristics in particular support this view: (1) colour, (2) the relative shortness of the sepals, (3) the extreme exertion of the column. As against this hypothesis, *A. exsertus* flowers in the autumn and *A. caudatus* in late winter and spring. I have, however, on rare occasions seen them flowering together (Port Jackson bushlands). But whatever its origin, the form described above is sufficiently distinctive to merit at least a varietal name.

### III. CALADENIA CARNEA R.Br. vars. MINOR and EXIGUA.

These two forms, originally described for New Zealand as *C. minor* Hook. f. and *C. exigua* Cheesmn., respectively, are not uncommon in Australia, and are now known as *C. carnea* var. *minor* (Hook. f.) Hatch and *C. carnea* var. *exigua* (Cheesmn.) Rupp. Both have the essential characters of *C. carnea*, the variations of which were discussed by the present writer in these PROCEEDINGS, lxxi, 1946, pp. 278-81. Both have quite recently been recorded in the northern suburban area of Sydney. But for its occurrence in New Zealand, where the larger forms of *C. carnea* are unknown, I doubt whether *C. carnea* var. *minor* would ever have been singled out for varietal rank, for it is in Australia linked up with larger forms by abundant intermediates. *C. carnea* var. *exigua*, however, is far more distinctive, the solitary marginal callus at the base of the midlobe on each side, and the entire margin of the lobe in front of the callus, rendering it easily recognizable. The lateral lobes of the labellum in the Sydney flowers are coloured bright rose. I am indebted to Capt. J. D. McComish of Wahroonga for calling my attention to this form.

*C. carnea* var. *minor*: Berowra and Cowan, New South Wales, ix.1946 (A. R. and H. M. R. Rupp).

*C. carnea* var. *exigua*: Wahroonga, New South Wales, ix.1946 (D. Connolly).

## SUB-SURFACE PEAT TEMPERATURES AT MT. KOSCIUSKO, N.S.W.

By J. A. DULHUNTY, D.Sc., Commonwealth Research Fellow in Geology,  
University of Sydney.

(One Text-figure.)

[Read 27th November, 1946.]

## INTRODUCTION.

The Kosciusko Plateau is a remnant of an early Tertiary peneplain, elevated by late Tertiary uplifts to a height of 6,000 to 7,300 feet above sea-level, and extensively dissected by subsequent erosion (Andrews, 1910). The plateau, representing the highest country in Australia, was glaciated during Pleistocene time (David, 1908; Browne, Dulhunty and Maze, 1944); and an alpine environment now exists, although glacial conditions have disappeared.

The highest portions of the plateau are covered with snow from eight to nine months of the year, and snow patches occasionally survive from one winter to another. During summer there is an abundant growth of vegetation (McLuckie and Petrie, 1927), and some small forms of animal life are active. Soils consist mainly of sand and gravel derived from granite which is the principal rock-type, although restricted outcrops of phyllite, occurring along the crest of the Main Divide, give rise to sandy clay. On slopes and hill sides the surface layer of soil, 6 to 18 inches deep, is of dark colour due to accumulation of humus. Peat formation occurs in upland swamps situated on undissected portions of the plateau where drainage is obstructed by moraines and topographical features produced by glaciation. Each winter the swamp vegetation is buried beneath snow, and compressed into a fibrous mat to which new growth is added each summer. Owing to the high level of swamp water and low temperatures, the rate of accumulation of plant debris exceeds that of decay, and, in some places, immature peat beds have been built up to a depth of 15 feet.

A preliminary investigation of peat temperatures was undertaken, as nothing was known of the sub-surface temperature conditions during summer and winter on the Kosciusko Plateau; and it appeared that results might be of value in the study of peat formation, biological problems, development of soils, and weathering of rock by frost action.

## TEMPERATURE DETERMINATIONS.

The investigation was carried out in a slightly elevated peat bed at the southern side of a swampy area on a headwater tributary of the Snowy River between Etheridge Range and Mt. Clark, in a valley to the north of, and beneath, Seaman's Hut. The peat bed is situated N. 56° E. from Mt. Kosciusko and S. 11° W. from Mt. Clark, at an elevation of 6,200 feet above sea-level. The position was chosen as it represents average conditions on the plateau, and results should be more or less typical for swamp lands of similar elevation.

On the 22nd January, 1945, a hole 6 feet 6 inches deep was excavated in the peat bed which was 6 feet thick, with gravel at its base. Three horizontal bore holes, 3 inches in diameter and 5 feet long, were made in one wall of the excavation at depths of 9 inches, 3 feet, and 6 feet from the surface, as illustrated in Figure 1. As soon as the holes were completed, maximum- and minimum-recording thermometers were placed at the ends of the holes which were then plugged with peat removed during boring. After seven days the thermometers were taken out, and the maximum temperatures, recorded at the three levels in the peat, were noted. The thermometers were then replaced in the bore holes which were plugged as before, and the excavation was filled in and allowed to remain through the winter when the peat bed was covered with snow. On the 21st January, 1946, the excavation was opened up, the thermometers withdrawn from the bore holes, and the minimum temperatures, recorded at the different levels, were observed.

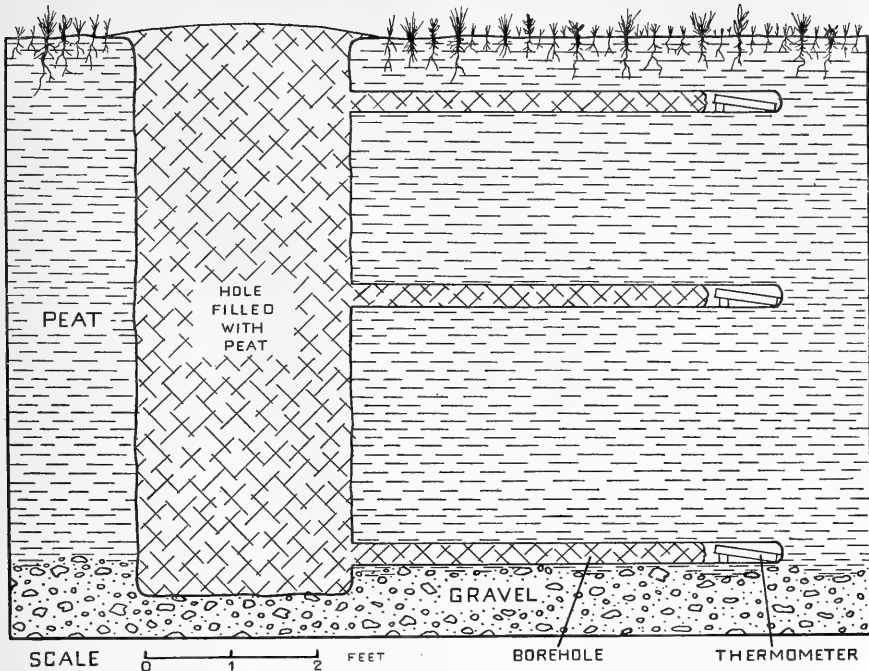


Fig. 1.—Method of determining sub-surface temperatures in peat bed.

The thermometers were standardized before and after the investigation by packing in ice for 24 hours to find amounts of error at 32°F., and readings were then taken in water at 41° and 52°F. The differences between readings, amounting to less than 1°F., were the same at the three different temperatures, indicating that the error for each thermometer was constant over the temperature-range employed. Actual readings recorded in the peat were converted to true temperatures by correcting for the error in each thermometer. The summer and winter temperatures, correct to ¼°F., are shown in Table 1.

TABLE 1.  
*Summer and Winter Temperatures in Peat Bed at Mt. Kosciusk.*

Position in Peat Bed.	Sub-Surface Temperatures.	
	Maximum recorded between 22nd–29th Jan., 1945.	Minimum recorded between 29th Jan., 1945–21st Jan., 1946.
At surface .. ..	63·00° F.	32·00° F.
9 inches down .. ..	50·50° F.	34·00° F.
3 feet down .. ..	44·25° F.	36·50° F.
6 feet down .. ..	43·75° F.	38·50° F.

The summer surface temperature of 63°F. was the average maximum daily temperature recorded on the surface of the ground, shaded by grass and herbage, during three weeks in January, 1945. The winter surface temperature was taken at 32°F., as the ground is covered with snow in which a temperature of 32°F. is maintained by equilibrium between heats of melting and freezing of ice and water. This was verified, to a certain extent, by the fact that the temperature at the base of a large snow patch, some 20 feet deep, was found to be exactly 32°F.

Extrapolation of the results, in the case of peat beds thicker than the one investigated, suggests that a temperature of 41° to 42°F., with very little seasonal variation,

exists at depths below 6 feet. It would appear, however, that extrapolation should not be carried below the base of any peat bed, as temperatures in underlying material may vary from place to place, depending on thickness of gravel separating peat from solid rock and the circulation of ground water. Very little movement of water takes place in the peat, but free circulation in underlying gravel may cause considerable seasonal variation in temperature below its base.

#### CONCLUSIONS.

In drawing conclusions from the preliminary results recorded in this paper, it is necessary to take into consideration the fact that they represent conditions which existed in one particular peat bed at the end of January, 1945, and during the ensuing winter. The figures for summer conditions represent the temperature gradient in the peat at the time when readings were taken. It is probable that the temperature at deeper levels (3 to 6 feet) would increase towards the end of summer, owing to the well-known lag in seasonal adjustment of soil temperatures (Moore, 1910). The winter temperatures, representing the minimum temperatures reached at different levels, can not be regarded as a gradient because they probably obtained at different times during the winter. While covered with snow, the ground would lose heat accumulated in summer, and the minimum temperature of 38.5°F. at 6 feet was probably reached at the end of winter—or even after the snow had disappeared, but before warmth from summer conditions penetrated to the deeper levels.

The extent to which the results may be taken as representative of the plateau area above about 5,500 feet is debatable until further results have been obtained at various elevations in different places. It appears probable, however, that sub-surface temperatures at depths greater than 9 inches in swampy areas and on hill sides of gentle slope rarely fall below 32°F., although very low temperatures (possibly approaching zero) are experienced at the surface as a result of frosts and blizzards towards the end of summer, before winter snow commences to lie on the ground. When covered with snow, the ground is shielded from the extremely low temperatures (below zero) which frequently occur in winter, and its surface appears to be maintained at the equilibrium temperature of 32°F.

Data regarding sub-surface temperatures have important applications in the study of peat formation. It is evident that the formation of peat on the Kosciusko Plateau is largely due to repression of organic decay by anaerobic conditions and low temperatures prevailing throughout the year at depths below 2 feet in the peat beds. On slopes and hill sides, decay is arrested while winter snow covers the ground; but in summer the water level falls below the surface, and warmer aerobic conditions allow decay to proceed more rapidly than in swampy areas, producing a high-humus soil rather than a peat.

Disintegration of rocks by frost action (expansion of water as it freezes in cracks and interstitial spaces) would appear to be limited to exposed rock surfaces, as the foregoing results suggest that sub-surface temperatures in saturated soil do not fall to 32°F. During winter, when frost action would be most destructive, the process would not be active on surfaces covered with snow (most of the plateau), as alternate freezing and thawing would not occur. In spring and autumn, melting and freezing of ice and water does take place over practically the whole region; but these periods are so short, owing to the long winter, that weathering by frost action is not extensive. This is evident at Lake Albina and the Blue Lake where glaciated surfaces of granite, covered with snow throughout winter, have not suffered greatly from frost action since they were smoothed and grooved by Pleistocene glaciers. Rocks subjected to abnormal weathering by frost action are those standing above the general surface of snow. Evidence of this is seen at high, rocky points such as Mts. Etheridge, Townsend and Gungartan, where granite has been shattered into irregular blocks and fragments.

Notes on the biological significance of results, recorded in this paper, were kindly supplied by the following writers:

*S. J. Copland, B.Sc.*—The observations are of particular interest from the standpoint of low temperature tolerance and conditions of hibernation in reptiles. At least six species of lizards and two of snakes are non-migratory and undoubtedly live the year

round on the high plateau country above 5,000 feet. All the reptiles are small enough (except *Denisonia superba*, and even this snake is much larger at lower altitudes) to avail themselves of the advantageous surface-mass ratio in adsorbing heat. Less work appears to have been done on the behaviour of reptiles at low temperatures with associated problems of hibernation and survival than at critical thermal levels.

The experiment made at an elevation of 6,200 feet, in a typical swampy area on the high plateau country, shows that the minimum winter temperature, a foot below the surface, is slightly more than 2°F. above freezing point, so that the hibernating reptiles at this depth have at no time to undergo the risk of formation of ice crystals in the body and almost certain death. This freezing would not occur even at 32°F. because of the essential presence in the body fluids of substances which lower the freezing point. Mt. Kosciusko reptiles almost certainly hibernate between depths of 9 inches and 3 feet where, the results show, they would have a margin of from 2° to 4.5°F. above freezing point. Although the minimum temperatures of 34° and 36.5°F. recorded at these depths must occur for only part of the winter, it seems certain that they are approached over most of the season, the temperature of 32°F. being rapidly adopted at the ground surface. A margin above freezing point is therefore essential because, while reptiles can successfully endure temperatures below this point for certain periods, exposure for months to freezing conditions could only be expected to cause death from chilling, with formation of ice crystals in the body, increased viscosity of body fluids, checked metabolism, and other disadvantageous physical and chemical changes.

*F. V. Mercer, B.Sc.*—The Kosciusko winter environment is difficult as the ground is covered with snow, air temperatures frequently fall below zero, and desiccating winds are a common feature of the habitat. Vegetative plant life, which can not withstand such conditions, passes the winter in a dormant phase. An examination of the swamp plants indicates that the majority are hemicyptophytes or geophytes with regenerating buds beneath the soil surface. Annuals are not common, and the deciduous habit is absent.

It is significant that the minimum soil temperature in the swampy area investigated does not fall below 32°F. The dominant type of habit is associated with this. The blanketing effect of the snow enables many plants to survive the winter. With the onset of warmer conditions a rich vegetation springs up from basal buds buried at, or near, the soil surface.

*K. E. W. Salter, B.Sc.*—Animal ecology demands a knowledge of the various controlling factors prevailing in the environment. The bionomics of insects can be largely correlated with temperature. An ecological study of the insect fauna of the Kosciusko region requires a knowledge of maximum and minimum temperatures, over the yearly cycle, in peats and soils. Many of the insects have subterranean larval stages, and it is most interesting to have so clearly demonstrated the fact that temperatures, at a depth of 3 feet in the peat bed investigated, do not fall below 37°F. during the winter.

#### ACKNOWLEDGEMENTS.

The author wishes to acknowledge the assistance of Dr. W. R. Browne in the interpretation and preparation of results for publication, and to express his gratitude to Messrs. S. J. Copland, F. V. Mercer and K. E. W. Salter for their interest in the work and contributions to discussion.

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NOTES ON THE MORPHOLOGY AND BIOLOGY OF *APIOCERA MARITIMA* HARDY  
(DIPTERA, APIOCERIDAE).

By KATHLEEN M. I. ENGLISH, B.Sc.

(Thirteen Text-figures.)

[Read 25th September, 1946.]

INTRODUCTION.

*Apiocera maritima* was described by Hardy (1933) from 9 specimens collected in Queensland on coastal dunes along the foreshore.

The species is represented in the collections of the Australian Museum, Sydney, by 6 specimens, in the Macleay Museum at Sydney University by 7 specimens, and in the School of Public Health and Tropical Medicine, Sydney, by 2 specimens. For some of these the only locality given is New South Wales, for the others the localities given are on the coast, in the vicinity of Sydney, New South Wales.

The material which forms the subject of this paper was all collected on beaches near Narooma on the south coast of New South Wales.

OCCURRENCE.

All the larvae and most of the adults and pupae were collected on the beach at Mystery Bay, a few miles south of Narooma; some adults and pupae were found on intervening beaches; no other parts of the coast were visited.

Over a number of years intermittent visits were made to Narooma in the months of January, February and early March, adults being taken in each of these months, but there was no opportunity of observing for what further period they were on the wing. The first specimens were a pair taken on 1st March, 1932; another pair was taken in January, 1936. Many were taken in 1938 and 1939 when more preparation had been made for collecting and visits to the beach were more frequent. In January, 1938, and again in January, 1939, dozens of the flies were to be seen resting on the sand in the sun, flying lazily from place to place, and mating. Females were observed moving the apex of the abdomen on the dry sand so that a small depression was formed, but whether this was in preparation for egg-laying or whether eggs had already been deposited was not determined.

In January, 1937, two empty pupal cases were found in a sand-bank at the back of the beach at Mystery Bay, and a pupal case of a different type was found in a similar position on the surfing beach. This suggested that a further search on the sand might prove worth while, and this surmise proved to be correct, for in January, 1938, fifty pupal cases of the first type and twenty-three of the second type, which proved to be the Apiocerid, which is the subject of the present paper, were found at Mystery Bay. On 26th January, 1939, seventy-nine Apiocerid pupal cases were collected at Mystery Bay on a stretch of beach about a quarter of a mile in length, and a few days later sixty-three cases were collected in about half an hour on the same stretch of beach. Some of these were protruding from the wet sand between tide marks, where the flies had recently emerged from them, but most were lying on the dry sand at the back of the beach where they had been blown by the wind, many of these being very weathered. The numbers show what a very prolific breeding ground this spot must have been for a species belonging to a family that is poorly represented in collections, and for which the numbers recorded with descriptions are usually small.



In November, 1938, a special trip to Narooma was made for the purpose of searching for larvae, and a wire sieve with one-fourth of an inch mesh was used with the idea that the larvae might be found by sifting the beach sand. At first no larvae or pupae were found, the places selected for digging evidently being too far back on the beach. Next day, digging and sifting was done nearer high-water mark and 1 active white larva and 2 pupae were found. Some hours' work on the beach daily for ten days yielded 12 large and 6 similar, smaller larvae and 2 pupae, all presumed to be Apioceridae; also 3 Therevid larvae, and 12 larvae and 10 pupae of a Tabanid. The best results on any one day were 6 larvae and 2 pupae of Apioceridae and 2 Tabanid larvae, but on some days none were found. It was difficult to determine at what depth exactly the larvae were present in the sand as several spades full of sand were sifted at a time, but one was uncovered in the sand about three inches from the surface and all were found between two and ten inches down. In January, 1939, 7 larvae and 1 pupa were found by sifting sand.

Of the two pupae found in November, 1938, one was badly damaged by the spade, the other appeared undamaged but it died without emerging. Of the large larvae, four pupated, one was deformed and died, one failed to emerge, from one, a female Apiocerid emerged, and from the fourth, a male emerged; both larval and pupal exuvia of this male specimen were obtained. The pupal periods were twenty and twenty-one days.

The larvae are carnivorous and had to be kept in separate jars. They proved to be very hardy and could probably be reared to maturity under laboratory conditions reasonably easily. One larva, smaller than those which pupated, was kept in moist beach sand (occasionally changed) in a 2-oz. jar from November, 1938, till November, 1939, when a piece of earth-worm was put in the jar; the larva lived till October, 1940, but later died of neglect. Another larger larva, taken in February, 1939, was kept in a similar manner, and it was observed feeding on the piece of earth-worm put in the jar in November, 1939; this larva lived till October, 1940, but later, like the other, was neglected and died.

#### Eggs.

No eggs were found in the sand nor were any deposited by females in captivity, no suitable cages having been made for keeping them for egg-laying. In February, 1939, the female of a mating pair was captured; she was kept in a small jar and died six days later without depositing eggs. The body contents were removed, as is done with large-bodied Lepidoptera, to see if the specimen would keep better, for these flies often deteriorate because they become very greasy. Eggs formed a large part of the body contents; 69 large ones were obtained and small ones were also seen. They were a creamy colour, long and rounded at the ends, more or less elongated ovate in shape. The largest were 2 mm. in length and 1 mm. in width.

#### THE LARVA. Text-fig. 1.

The larva is white in colour, long and relatively slim; the largest one measured was 51 mm. in length and 3 mm. in width. The anterior and posterior segments are more or less cylindrical, and the middle segments are noticeably bead-like in shape. There are 12 segments exclusive of the head.

The prothorax is long, it tapers anteriorly and ends in a thickened collar which is broader on the dorsal side, and is covered with very small tubercles. The 2nd thoracic segment is about the same length as the 1st, the 3rd is shorter, and they are both cylindrical in shape. Each thoracic segment carries a pair of short hairs.

The first five abdominal segments are pear-shaped, thicker anteriorly and tapering posteriorly, with a slight constriction posterior to the middle in each one; the 1st segment is shorter than the succeeding ones; these segments give the characteristic bead-like appearance to the body. The 6th, 7th and 8th segments are long and more or less cylindrical. The apical segment is short and the ventral surface curves sharply upwards to meet the dorsal surface in an almost straight transverse keel, slightly chitinized. The anus is situated on the ventral surface, and the segment carries four pairs of hairs, the most posterior pair being much longer than the others. On abdominal segments 2 to 6 there is a suggestion of paired processes on the ventral

surface, marked more by semi-circular depressions than by actual protuberances. These marks are very slight on the 6th segment.

The body is longitudinally striated, and bears on each side a pair of longitudinal furrows, which are deep and well marked anteriorly, but less pronounced posteriorly. The thoracic hairs are situated in the ventral furrow on each side, and all the spiracles are situated laterally between the furrows. Towards the posterior end of each abdominal segment two semi-circular furrows on each side cross the lateral ones and mark out a small upraised area.

*The Head.* Text-figs. 6, 7 and 8.—The head is well developed, elongated, and the anterior portion is downwardly directed; it can be almost wholly protruded from the first thoracic segment, and it can be retracted into it for nearly half its length. The dorsal surface is strongly arched, the ventral surface being slightly rounded. Placed laterally and extending along the middle two-thirds of the head is a flat keel of transparent chitin; this, together with the rest of the head, becomes dark brown in the larval exuvia, and it gives the head a much broader and flatter appearance than is evident in the larva itself.

The dorsal surface of the epicranium is strongly chitinized, with two longitudinal dark marks showing the internal position of attachment of the more heavily chitinized dorsal rods of the vertical plate. To the centre of the posterior edge is articulated a long chitinized rod, which is very much flattened dorso-ventrally, slightly arched anteriorly, and bent and strongly arched posteriorly; it is nearly twice as long as the head and can be seen through the integument of the prothorax. Melin (1923), in the "Biology, etc., of the Swedish Asilids", calls this the "capsule rod". At each anterior lateral corner of the epicranium, there is a bud-like sensory organ, probably the antenna; some distance behind the antennae, nearer the lateral border on each side, is a long bristle.

The ventral surface of the epicranium is covered for the most part with unchitinized or lightly chitinized membrane, with a large chitinized shield-like ventral plate situated anteriorly. Situated on the membrane at each anterior lateral corner, is a short bristle, and close behind are two long bristles.

Laterally, the epicranium is bordered by the major portion of the lateral keel which extends at its full width from the anterior edge backwards past the middle, then tapers off, leaving bare the posterior portion of the epicranium.

Internally, the anterior median dorsal portion of the epicranium (Text-fig. 9) is occupied by a chitinized box-like structure bounded dorsally by the dorsal rods and the inner surface of the epicranium, laterally by the vertical plates, and ventrally by the ventral rods, which are joined by a narrow strip of thin chitin. Melin (1923) calls a similar structure in the Asilids the "pharynx support". If the membrane is removed from the ventral surface of the epicranium the posterior portion of the ventral rods can be seen extending beyond the ventral plate (Text-fig. 8), and articulated to them posteriorly can be seen also the tentorial rods which extend back into the prothorax. At the anterior edge of the pharynx support, the pharynx opens into the mouth cavity, and posteriorly it runs backwards just above the ventral rods. The oesophagus lies just above the tentorial rods and is apparently supported by them.

The anterior downwardly-directed portion of the head contains the mouth-parts; it is rounded anteriorly and divided vertically by the mouth cavity.

The dorsal surface is strongly arched and is armed with three long bristles on each side posteriorly, and one short bristle on each side anteriorly situated. In the median line, and attached posteriorly to the epicranium, is the labrum, on each side of which can be seen the posterior portion and part of the anterior portion of the heavily chitinized mandibles. On each side of these is a large, more or less triangular, membrane-covered part attached posteriorly to the epicranium; through the membrane can be seen heavily-chitinized parts, the most anterior of these probably representing the maxillae.

The ventral surface is slightly curved and membrane covered, with the chitinized parts showing through more or less faintly. A pair of triangular thickened membranous lobes occupy the posterior half, and in front of these, hanging downwards, is a pair of slender two-jointed bristles.

Laterally, the triangular lobes are bordered by the anterior part of the lateral keel. Also situated laterally is a pair of large two-jointed palpi (Text-fig. 13).

*Mouth-Parts.* Text-figs. 9 and 10.—The narrow labrum of clear chitin curves slightly downwards to a point anteriorly; it is thicker at the base, the under surface of which forms the dorsal border of the mouth opening; it is armed with dorsal spines near the apex and is toothed on the ventral surface near the base. Below the labrum, in the median line, is the narrow chitinized hypopharynx which is articulated posteriorly to the anterior end of the ventral rods, and is forked at the apex. Below this is the labium, a laterally-compressed structure with a narrow chitinized band above and an almost transparent lobe-like part below, which is covered with hairs and spines. The salivary duct opens below the hypopharynx and runs backwards below the ventral rods of the pharynx-support. Below this a strong muscular complex runs back from the labium.

On each side of the labrum are the strongly chitinized mandibles; the chitin is thick below and curves over above to form a longitudinal canal on the inner surface of each. Each mandible fits into a groove in the dorsal part of the maxillary mouth-part beside it. Below and in front of this groove, the inner membranous faces of the maxillary mouth-parts form the pre-oral cavity. The membrane in the posterior part of this cavity is lined with a criss-cross pattern of fine-toothed ridges; anteriorly, it is lined with fine hairs and filaments, and just below the mandibular groove it is lined with stronger branched filaments.

In slide mounts of the maxillary mouth-parts, near the apex of each, can be seen two sensory canals; one opens by a pore into the ventral part of the pre-oral cavity, and the other by a pore on to the exterior near the apex. Melin (1923) figures similar anterior pores in some species, but he does not mention them in the text, so it is not known whether they represent similar structures.

*The Spiracles.* Text-figs. 11 and 12.—The anterior spiracles are distinct and situated laterally near the posterior border of the prothorax. The posterior spiracles are large and situated laterally on the anterior part of the penultimate segment. There are also eight pairs of small spiracles situated laterally on the metathorax and abdominal segments 1 to 7. When the larva contracts, the anterior part of the mesothoracic and metathoracic segments folds over, and part of the fold goes on to the segment in front, so that the anterior spiracles can be covered in this way. The posterior part of each abdominal segment folds over and part of the fold goes on to the segment behind, the posterior spiracles often being covered in this way.

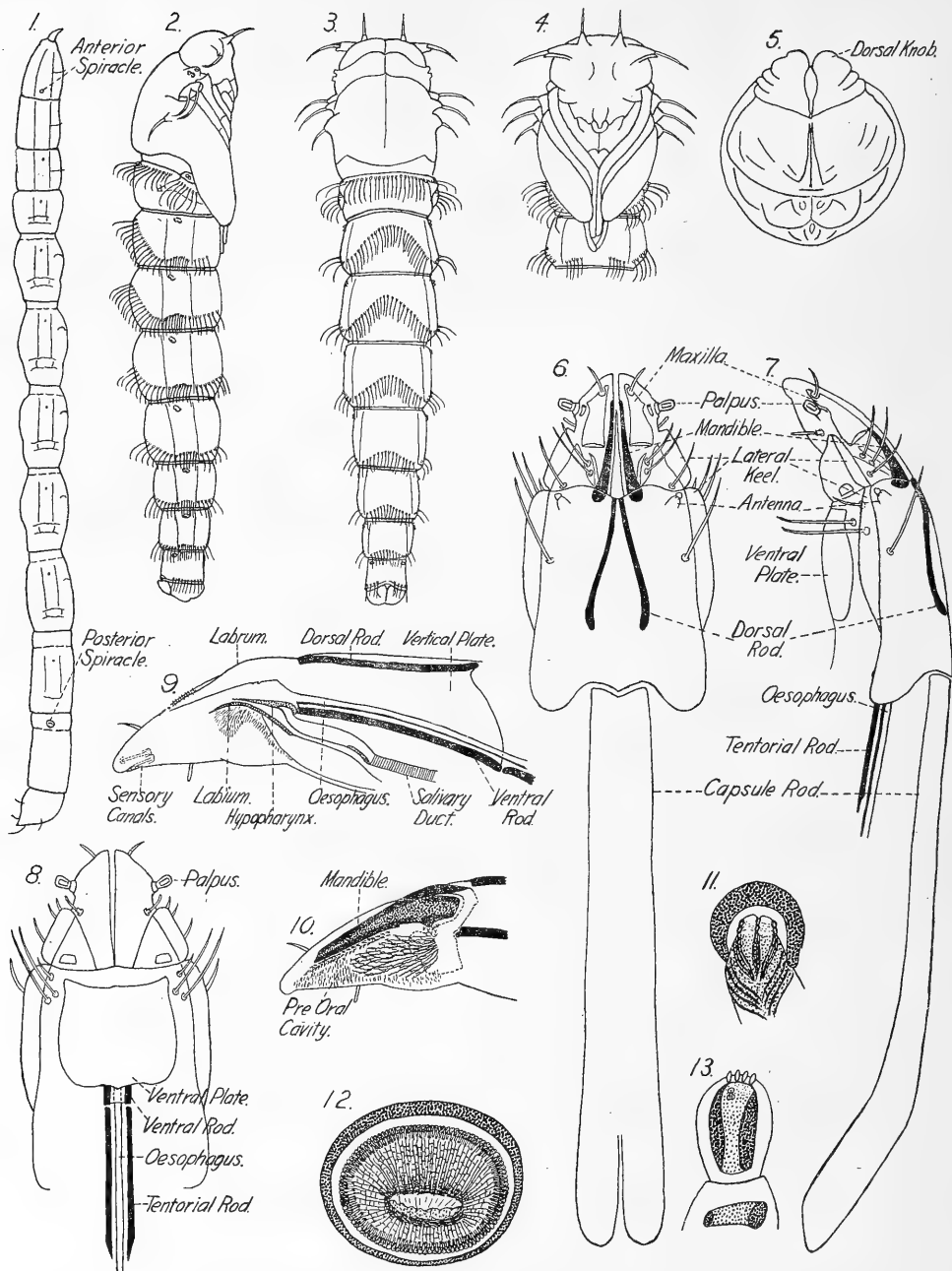
#### THE PUPA. Text-figs. 2, 3 and 4.

Pupal exuvia vary greatly in size, from 18 mm. to 28 mm. in length, and from 3 mm. to 5 mm. in width; in general, the large sizes are female and the small sizes are males, but the middle sizes may be either; size no doubt is dependent on food supply which for carnivorous larvae must vary considerably.

Male and female pupae can be distinguished though the differences are slight. In the female the abdomen is relatively stouter; also, on the 8th segment, the anal tubercle is well developed and the space between the bristles on the ventral surface is wide; in the male, the anal tubercle is undeveloped and the space between the bristles on the 8th segment is very narrow. There are slight differences also in the markings of the apical segment.

The head is armed with two pairs of strong bristles. The two anterior bristles are usually straight and forwardly directed, each being situated on a tall conical tubercle. The two posterior bristles are curved and directed laterally, each situated, together with a short blunt spine, on a larger conical tubercle.

The thorax is armed with three pairs of strong bristles. Two bristles are situated on adjacent squat tubercles at the base of each middle leg, and there is a single one on a low rounded tubercle at the base of each wing. The thoracic spiracle is elevated, with a well-defined reniform area, and there is a small, but definite, elevation just in front of the spiracle.



Text-figs. 1-13.—*Apiocera maritima*. 1. Larva, lateral view,  $\times 3$ . 2. Pupa, lateral view,  $\times 4$ . 3. Pupa, dorsal view,  $\times 4$ . 4. Anterior end of pupa, ventral view,  $\times 4$ . 5. Posterior end of male pupa,  $\times 16$ . 6. Head of larva, dorsal view,  $\times 30$ . 7. Head of larva, lateral view,  $\times 30$ . 8. Head of larva, ventral view,  $\times 30$ . 9. Vertical section of larval head, showing labrum and labium,  $\times 50$ . 10. Vertical section of larval head, showing mandible and pre-oral cavity,  $\times 50$ . 11. Anterior spiracle of larva, surface view,  $\times 55$ . 12. Posterior spiracle of larva, surface view,  $\times 55$ . 13. Palpus,  $\times 100$ .

The wing sheaths extend slightly beyond the basal abdominal segment, the apices of the fore-tarsi do not extend as far as the wings, the apices of the mid-tarsi extend beyond the wings, and the apices of the hind-tarsi extend well beyond the apices of the mid-tarsi and beyond the middle of the second abdominal segment.

The abdomen consists of nine segments, all armed with numerous strong bristles, except the last one, which is unarmed. The arrangement of the bristles varies considerably on the segments and the description will be clearer if the surfaces, instead of the segments, are taken separately.

*Dorsal surface.*—On the 1st segment the line of bristles runs near, and parallel to, the anterior edge. On the 2nd segment the line of bristles is placed towards the posterior edge laterally, and it curves sharply forwards to the centre of the back, where the apex of the curve is near the anterior edge of the segment. On each succeeding segment the lateral bristles are nearer the posterior edge and the curve diminishes, until the 7th segment, where the line of bristles is almost parallel to the posterior edge of the segment. On the 8th segment the centre is devoid of bristles, and those placed laterally are near, and parallel to, the posterior edge.

*Ventral surface.*—On the 1st segment there are no bristles. On the 2nd segment there are five or six bristles on each side and the centre is bare. On each succeeding segment the width of the bare part is reduced until, on the 7th segment, the line of bristles is continuous; on the 8th segment the centre is bare. On the ventral surface, on all segments, the line of bristles is placed near the posterior edge laterally and it curves forwards slightly in the centre.

*Lateral surfaces.*—The pleural ridge is well marked except on the 8th and 9th segments. On the first segment the bristles are borne on a marked swelling. On the 2nd segment the bristles are borne on a slight swelling, the line of bristles is placed towards the posterior edge of the segment and it curves forward slightly from the sides. On each succeeding segment the swelling and the curve diminish, and on the 8th segment, the bristles are practically parallel to the posterior edge of the segment. The number of bristles on the pleural ridge varies in different specimens, but it is always more than five.

The abdominal bristles are similar to the thoracic bristles but more slender; they are long and strong and on the anterior segments frequently sharply curved. On each succeeding segment they decrease in strength and curvature and on the posterior segments they are quite straight; each bristle is borne on a slender conical base. There are eight abdominal spiracles situated laterally towards the anterior edge of each segment, except the last; all are borne on small tubercles and have a reniform outline.

The apical segment has no outstanding characters.

The whole abdominal surface is covered with a network of raised lines, the general trend of which is longitudinal.

The morpho-type, consisting of the larval exuvia, together with its corresponding pupal exuvia and the imago, have been deposited in the Macleay Museum at the University of Sydney. Other specimens and slides used in the preparation of this paper have been deposited there also.

#### CONCLUSION.

There are apparently no previous records of the immature stages of the Apioceridae, and therefore the family is not included in keys for the identification of the larvae and pupae. The latest available key of this kind was published by Brues and Melander (1932), and in this the key for the immature stages of Diptera is based on Malloch (1917), and for the Orthorrhapha, it is unchanged except for some additions to include another family. In the same way, additions could be made to Malloch's key near the Asilidae to include the Apioceridae, using, for the larvae, the long penultimate segment, the variation in shape of the abdominal segments, and the lateral keel on the head; and for the pupae, the uniformity of the abdominal bristles and the unarmed apical segment.

It remains to be seen whether the characters of this species are typical of the family or whether the environment has given rise to specialized characters. However, the description of the immature stages of this one species tends to confirm the position of the Apioceridae as a separate family in the superfamily Asiloidea, where it has been placed on adult characters.

#### ACKNOWLEDGEMENTS.

For the opportunity to prepare this paper the writer is indebted to Dr. E. A. Briggs of the Department of Zoology, University of Sydney, who made available laboratory accommodation at the Department; without this help the work could not have been undertaken. The writer is also indebted to Mr. A. R. Woodhill of the Department of Zoology for helpful criticism of the paper, to Miss A. G. Burns of the same Department for help and advice with the drawings, and to Mr. G. H. Hardy of the University of Queensland for the identification of the adult flies.

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## A REVIEW OF THE PHYLOGENY AND CLASSIFICATION OF THE LEPIDOPTERA.

By A. JEFFERIS TURNER, M.D., F.R.E.S.

(Ninety-six Text-figures.)

[Read 30th October, 1946.]

## INTRODUCTION.

It would be impossible for one who has not access to the necessary documents to give a history of the classification of the Lepidoptera. Fortunately a brief reference to three well-known works will give sufficient historical background to this essay.

The first is "A Manual of British Butterflies and Moths", in two volumes, the first published in 1857, the second in 1859, by H. T. Stainton. From this old work, which breathes a charm unknown to modern writings, I extract the following classification. To facilitate its understanding I have added a few words in parentheses.

Rhopalocera.	Geometrina.
Papilionidae (including Pieridae).	17 families.
Nymphalidae.	Pyralidina.
Erycinidae.	17 families (including Hypenidae,
Lycaenidae.	noctuid genera <i>Earias</i> and
Hesperiidae.	<i>Halias</i> , Nolidae, and glyphi-
Heterocera.	pterygid genera <i>Choreutis</i> and
Sphingina.	<i>Simaethis</i> ).
Zygaenidae.	Tortricina.
Sphingidae.	9 families.
Sesiidae (clear-winged Sphingidae).	Tineina.
Aegeriadae.	Exapatidae (Oecophoridae).
Bombycina.	Tineidae.
Hepialidae.	Micropterygidae.
Zeuzeridae.	Hyponomeutidae.
Notodontidae.	Plutellidae.
Liparidae (Lymantriadae).	Gelechidae.
Lithosiadae (Arctiadae).	Oecophoridae.
Chelonidae (Arctiadae).	Glyphipterygidae.
Bombycidae (Lasiocampidae).	Argyresthidae.
Saturniidae.	Gracilariidae.
Platypterygidae (Drepanidae).	Coleophoridae.
Psychidae.	Elachistidae.
Cochliopodidae (Limacodidae).	Lithocolletidae (Gracilariadae).
Noctuina.	Lyonetidae.
Trifidae.	Nepticulidae.
15 families (including the Cymato-	Pterophorina.
phoridae).	Pterophoridae.
Quadrifidae.	Alucitina.
9 families.	Alucitidae (Orneodidae).

Just as the lineaments and character of a future adult are already apparent in a young child, so we may see here the early stage of our modern classification. Looked at with scientific impartiality its excellencies outweigh its evident defects. Especially in the Tineina, for which Stainton was most directly responsible, while in other groups

he borrowed from other writers, we have a list of families closely corresponding to that given in the most recent work of Meyrick, who was himself primarily a microlepidopterist. The Rhopalocera and Bombycina call for little criticism. On the other hand, it must be admitted that Stainton's Sphingina consists of three widely unrelated families. His Noctuidina are rightly separated into Trifidae and Quadrifidae,\* but, like the Geometrina, Pyralidina and Tortricina divided into families, which are based on no structural characters, and I have not thought it necessary to transcribe their names.

In 1895, just thirty-six years later, a great advance in our knowledge was made by the appearance of "A Handbook of British Lepidoptera" by Edward Meyrick with the following classification.

Caradrinina.	Pyralidina.
Arctiidae.	Phycitidae.
Caradrinidae (Noctuidae).	Galleriidae.
Plusiidae (Noctuidae).	Crambidae.
Oceriadae (Lymantriadae).	Pyraustidae.
	Pyralidae.
Notodontina.	Pterophoridae.
Hydriomenidae (Larentiadae).	Orneodidae.
Sterrhidae.	
Geometridae.	Psychina.
Monocteniidae (Oenochromidae).	Psychidae.
Selidosemidae (Boarmiadae).	Zeuseridae (Cossidae).
Polyplocidae (Cymatophoridae).	Zygaenidae.
Sphingidae.	Heterogeneidae (Limacodidae).
Notodontidae.	
Saturniadae.	Tortricina.
	Epiblemidae (Eucosmidae).
Lasiocampina.	Tortricidae.
Drepanidae.	Phaloniadae.
Endromidae.	Trypanidae (Cossidae).
Lasiocampidae.	
	Tineina.
Papilionina.	Aegeriidae.
Nymphalidae.	Gelechiidae.
Satyridae.	Oecophoridae.
Erycinidae.	Elachistidae.
Lycaenidae.	Plutellidae.
Pieridae.	Tineidae.
Papilionidae.	
Hesperiadae.	Micropterygina.
	Hepialidae.
	Micropterygidae.

Here we have a classification based on defined structural characters. While characters derived from the structure of the tongue, palpi, antennae (especially in the male), legs (especially the posterior pair), wing-coupling apparatus, and the presence of scale-tufts on the forewings are not neglected, the definitions depend chiefly on the neuration, which has been studied with much care. Except in the Tineina, the families have been firmly established, if we omit the inclusion of the Nolidae and some noctuid genera in the Arctiidae, and the unnecessary division of the Noctuidae into two families. The superfamilies do not rest on such a secure basis. The Notodontina, Lasiocampina and Psychina are open to criticism as heterogeneous groups. The inclusion of the Cossidae in the Tortricina has already been abandoned (in 1927), and in my opinion the separation of the Tortricina from the Tineina is not justified.

\* These words are good Latin, just as trifid and quadrifid are good English, and have no connection with Greek names ending in -idae or -inae. It is an error to transliterate them into Trifinae and Quadrifinae, as has been done by some.



A noteworthy characteristic of Meyrick's work was that he never accepted his own classification as final, and in "A Revised Handbook of British Lepidoptera" published in 1927 he introduced several changes.

## Caradrinina.

Arctiadae.  
 Nolidae.  
 Hylophilidae (several noctuid genera).  
 Caradrinidae.  
 Plusiadae.  
 Oceriadae.

## Notodontina.

Sterrhidae.  
 Geometridae.  
 Hydrimenidae.  
 Monocteniidae.  
 Selidosemidae.  
 Polyplocidae.  
 Sphingidae.  
 Notodontidae.  
 Saturniadae.

## Papilionina.

Papilionidae.  
 Nymphalidae.  
 Satyridae.  
 Erycinidae.  
 Lycaenidae.  
 Pieridae.

## Hesperiana.

Hesperiidae.

## Drepanina.

Drepanidae.

## Pyrалidina.

Phycitidae.  
 Galleriadae.  
 Crambidae.  
 Pyraustidae.  
 Pyralidae.  
 Pterophoridae.

## Lasiocampina.

Endromidae.  
 Lasiocampidae.

## Psychina.

Heterogeneidae.  
 Zygaenidae.  
 Psychidae.  
 Zeuzeridae.

## Tortricina.

Phaloniadae. Tortricidae.  
 Eucosmidae.

## Tineina.

Group 1. Gelechiidae. Blastobasidae.  
 Cosmopterygidae. Oecophoridae.  
 2. Orneodidae.  
 3. Aegeriadae. Heliodinidae.  
 Heliozelidae. Glyphipterygidae.  
 4. Elachistidae. Scythridae.  
 Douglasiadae. Hyponomeutidae.  
 5. Coleophoridae. Epermeniadae.  
 Gracilariadae. Plutellidae.  
 6. Lyonetiadae. Lamproniadae.  
 Tineidae. Adelidae.

## Nepticulina.

Nepticulidae.

## Micropterygina.

Hepialidae.  
 Micropterygidae.

## CRITICISMS OF MEYRICK'S CLASSIFICATION.

We owe a great debt to Meyrick's work. Whatever future changes may be made, and no classification can remain static, while our knowledge continues to increase, we are indebted to him for a classification based on structure. For this he is entitled to our respect. It should be our purpose to build on the foundation he has laid, keeping an open mind on matters that may appear doubtful, and endeavouring to be guided only by facts, knowing well that any classification that we may propose will itself be changed by those who may come after us. In this spirit I propose to offer the following criticisms.

(1). In his revised classification, the family Arctiadae has been purged of extraneous elements, and the family Nolidae has been recognized as a distinct family. His conception of the family Hylophilidae is unfortunate, being based on a single character, the long anastomosis of 8 of the hindwings with the cell, a character which occurs in wholly unrelated families such as the Larentiadae, Oenochromidae, Boarmiadae, Drepanidae, and in the genus *Stilbia* recognized by himself as a noctuid. These are instances of "parallel evolution", which is of common occurrence in the Lepidoptera. The genera

of his "Hylophilidae" are close allies of other noctuid genera, in which this anastomosis is short and sub-basal.

(2). The Noctuidae is a very homogeneous family and its division into two families on a character which is not always distinctive is not justified.

(3). The superfamilies Notodontina and Psychina contain families not closely related. This and the following criticisms are more fundamental and will be discussed at some length.

(4). The position of the Papilionina and their severance from the Hesperiana require closer examination.

(5). The separation of the Tortricina from the Tineina is not justified.

(6). The morphological differences between the Hepialidae and the Micropterygidae are too great to allow their inclusion in a single superfamily.

(7). The classification lacks major divisions.

#### THE MORPHOLOGY OF THE WINGS OF LEPIDOPTERA.

Although Meyrick's classification depends mainly on the neuration, he makes no use of some of its most important features. This is well shown by Figure 1 copied from his Revised Handbook. His assumed type of neuration shows in the forewing three anal veins, 1a, 1b and 1c (which is Cu2), a central cell from which arise veins 2 to 11, and a subcostal vein 12. The hindwing differs in having only six veins arising from the central cell. He mentions the occasional occurrence in some earlier forms of a forked "parting-vein" traversing the cell of both wings and another "parting-vein" cutting off the upper posterior area of the cell in the forewing. So far good: but these complications are denied any importance in the classification of the Lepidoptera, though he admits that they may have some bearing, when considering its relationship to other orders.

In my opinion the variations in the peripheral veins, which Meyrick has studied so carefully, give good generic characters, but are of minor importance in showing the affinities of families and superfamilies, which are often better indicated by the basal vein trunks. His assumed type of neuration, in spite of its apparent simplicity, is not primitive, but has resulted from very remarkable changes affecting the really primitive form. The whole course of evolution in the lepidopterous wing has been from complexity towards simplicity by loss or coalescence of veins. It has been an evolution by asthenogenesis, and has often followed parallel lines in groups not nearly akin. Confining ourselves for the moment to the Lepidoptera Heteroneura, I present Figure 2 as the primitive neuration. While not the exact neuration of any existing genus, it combines the most primitive characters of several genera of Cossidae. Here the forewing has four main trunk veins, the subcostal, the radial with five branches, the median with three, and the cubital with three, together with two concurrent anal veins. In the hindwing there are three anal veins but only two radial, the radial sector being unbranched and the first radial running into the subcostal. All these longitudinal veins are formed around the tracheae of the pupal wings. In addition, there are three cross-veins which arise independently of the tracheae. This will be made clearer by the accompanying diagram (Fig. 3). The radius divides at the first radial fork into the first radial and the radial sector; the latter divides at the second radial fork, and these branches again divide into the second and third radial and the fourth and fifth radial respectively. The discoidal cell or areole is completed by an inter-radial cross-vein. Within the main cell the median divides into two branches, each of which again divides into two, the fourth branch joining with the uppermost cubital branch to form a compound vein. The median cell is closed by the intermedian cross-vein, and the main cell, in which it is enclosed, is completed by the radio-median cross-vein. The inter-radial cross-vein tends to disappear in many groups, being replaced by anastomosis between R3 and R4. This completes the areole.

By its conciseness and freedom from ambiguity the numerical notation adopted by Meyrick is well adapted for the description of generic and specific differences, but is defective when applied to the definitions of higher groups. In this review I have accordingly adopted the notation proposed by Comstock and Needham as modified by Tillyard. The following scheme illustrates the relationship of these two notations.

Forewing.				Hindwing.			
Vein 12	..	..	Subcostal	Vein 8	..	..	Subcostal
"	11	..	First Radial	(Wanting)	..	..	First Radial
"	10	..	Second "	"	7	..	Radial Sector
"	9	..	Third "	"	6	..	First Median
"	8	..	Fourth "	"	5	..	Second "
"	7	..	Fifth "	"	4	..	Third "
"	6	..	First Median	"	3	..	Cubital 1a
"	5	..	Second "	"	2	..	" 1b
"	4	..	Third "	"	1a..	..	" 2
"	3	..	Cubital 1a	"	1b..	..	Conjoint first and second Anals
"	2	..	" 1b	"	1c..	..	Third Anal
"	1a..	..	" 2				
"	1b..	..	First Anal				
"	1c..	..	Second "				

## THE HOMONEURA.

The Lepidoptera fall into two natural divisions or suborders the Homoneura (or Jugata) and the Heteroneura (or Frenata). In the former the radial sector divides into four (rarely three) veins in both fore- and hindwings; and wing-coupling is effected by a process at the base of the dorsum of the forewing known as the jugum. The suborder is divisible into two superfamilies, the Micropterygoidea and the Hepialidoidea, the former being the more primitive, and composed of three families. Although these are subfamilies in Meyrick's classification (Meyrick, 1912), the differences between them are sufficient to justify family rank. The most primitive family is the Micropterygidae. Its neuration, shown in Figure 4, is in most respects similar to that of the most primitive family, the Rhyacophilidae, of the Trichoptera, though with a few not unimportant differences. Both neurations show striking resemblance to that of *Belmontia*, a fossil wing from the Upper Permian. For this, Tillyard has created the order Paramecoptera, which he believes to be the common ancestor of the Trichoptera and Lepidoptera (Tillyard, 1919).

The family Micropterygidae is primitive not only in neuration; but they are the only Lepidoptera that possess functional toothed mandibles and maxillae with primitive short galea and lacinia as well as with long five-jointed palpi (Philpott, 1927). The Eriocranidae have lost the mandibles in the imago, and the maxillae are specialized by the loss of the lacinia and the transformation of the galea into a short haustellum, although the palpi are similar. In the forewing the inter-radial cross-vein is not developed and consequently there is no areole. The larvae of the two families differ greatly. In the Mnesarchaeidae the mandibles are absent, the maxillae have a well-formed haustellum with very small three-jointed palpi. The radial sector is three-branched in both wings and there is no areole. It should be noted that in Figure 4 the hindwing differs from the forewing in several points. The first radial runs into the second subcostal and its basal portion is obsolete; the second cubital is scarcely developed; and the anal veins have been much reduced.

The neuration of the Hepialidae is remarkably constant (Philpott, 1926). With the exception of the presence of a weak branch of the subcostal of the forewing in *Sthenopsis*, which I can confirm from my own observation, and the degraded neuration of the hindwing in *Elthamma (Perissectis)*, which is present only in the male, and therefore of little significance, there seem to be no noteworthy variations. In Figure 5 both wings are alike except in the anal area. The median fork is always near the base, and an intermedian cross-vein closes the median cell, but there is no areole. In the Micropterygoidea the median fork is more distal, and intermedian cross-vein and median cell are absent. In the Hepialidae the first radial is always simple, and the junction of the fourth median with the uppermost branch of the cubital is strongly angled.

Recently in Australia and South Africa genera have been discovered which are rather closely allied to the Hepialidae, but have been considered to represent new

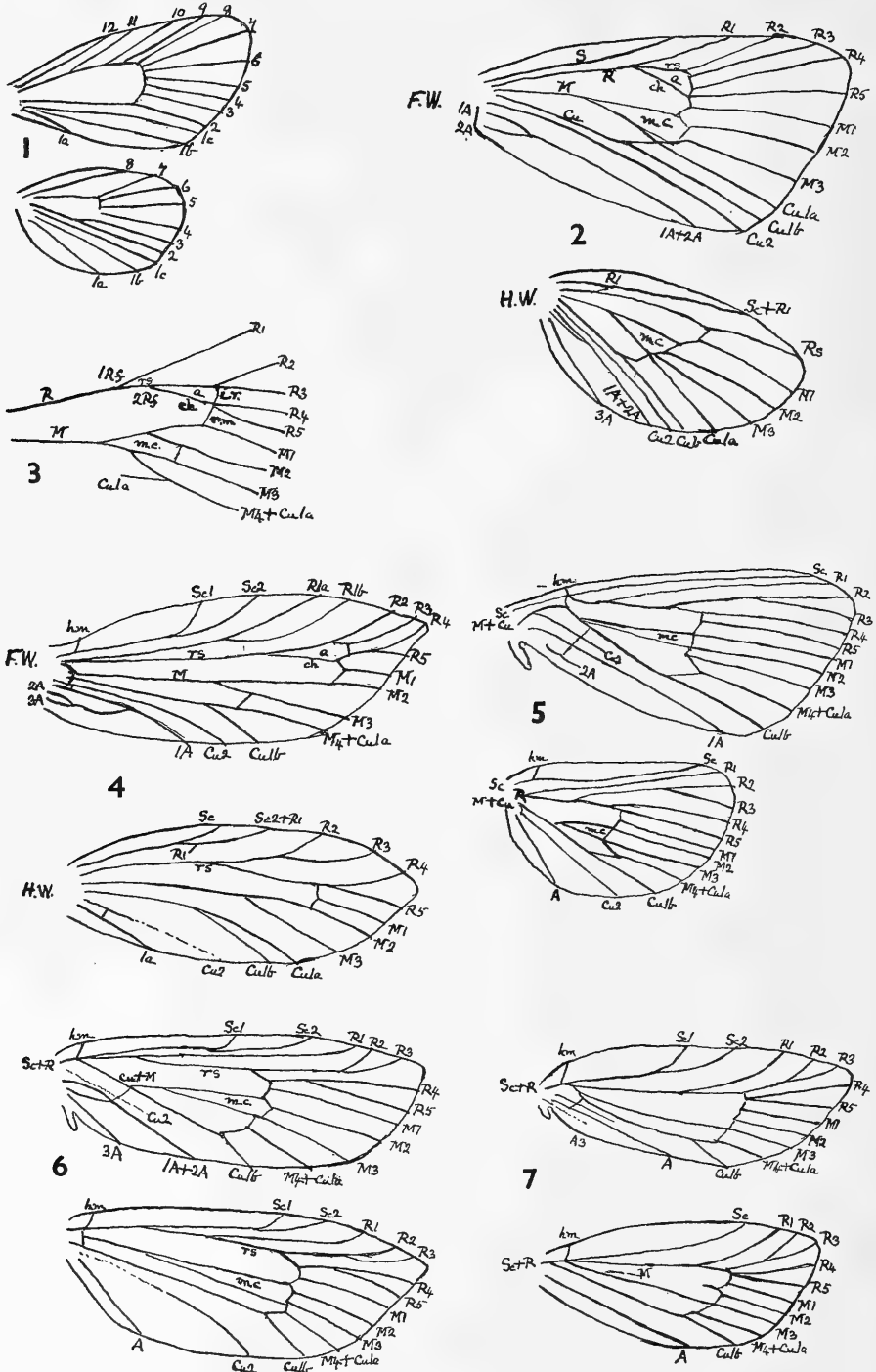


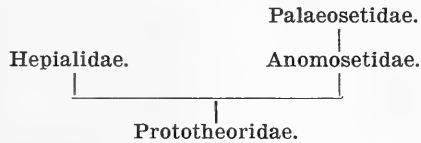
Fig. 1.—Meyrick's assumed type of neuration. Fig. 2.—Diagram of protocossid neuration. Fig. 3.—Diagram of radial and median veins. Fig. 4.—*Sabatinka incongrua* Wlk. (after Philpott). Fig. 5.—*Trictena argentata* H-Sch. Fig. 6.—*Prototheora* sp. (after Philpott). Fig. 7.—*Anomoses hylecoetes* Turn.

Sc., Subcostal; R., Radial; M., Median; Cu., Cubital; A., Anal; a., Areole; m.c., Median cell, i.r.f., First radial fork; 2.r.f., Second radial fork; second radial fork; ch., Chorda; r.s., Radial sector; i.r., Inter-radial; r.m., Radio-median; i.m., Intermedian.

families (Turner, 1918; Philpott, 1928). Their neururation is shown in Figures 6, 7 and 8. Their differences from Hepialidae and each other may be tabulated as follows:

<i>Hepialidae.</i>	<i>Prototheoridae.</i>	<i>Anomosetidae.</i>	<i>Palaeosetidae.</i>
Subcostal rarely forked in f.w., never in h.w.	Subcostal forked in both wings.	Subcostal forked in f.w. only.	Subcostal forked in f.w. only.
Median vein forked.	Median vein forked.	Upper branch of median absent.	Upper and lower branches of median absent.
M4 strongly angled with <i>Cu1a</i> .	M4 slightly angled with <i>Cu1a</i> .	M4 slightly angled with <i>Cu1a</i> .	M4 absent.
F.w. with one or two anal veins, 1A and 2A sometimes looped.	F.w. with three anal veins, 1A and 2A looped.	F.w. with two anal veins not looped.	F.w. with one anal vein.
Maxillae and palpi rudimentary.	Maxillae with small haustellum and rudimentary palpi.	Maxillae with small haustellum and short palpi.	Maxillae absent.
Tibial spurs absent.	Tibial spurs present.	Tibial spurs present.	Tibial spurs absent.

In my opinion we must either include all these groups in the Hepialidae, or recognize four families, of which the Prototheoridae and Anomosetidae are the most nearly akin. When we consider the amount of difference that separates many families in the Heteroneura, I think we should not hesitate to adopt the latter alternative. This has the advantage of making clearer the mutual relationship of the groups involved, which may be represented as follows:



THE HETERONEURA.

SOME NEURATIONAL CHARACTERS OF FUNDAMENTAL IMPORTANCE.

The classification of the Heteroneura is a much more difficult problem, and cannot be approached without a preliminary discussion of some points in their structure, which have not, I think, as yet received sufficient consideration.

In this classification all structural characters should be carefully considered, not excluding those of the larval and pupal stages, but we have to depend principally on differences in the neururation of the wings. On account of the tendency to the loss of veins in almost all the families, and of course also in the superfamilies, we must always be on our guard against the fallacies of parallel evolution and asthenogenesis. Against this we have two safeguards. Most of the families are natural groups well defined by a combination of characters and having their extreme forms more or less connected by intermediate genera. In them we may observe the process of simplification by asthenogenesis, the intermediate steps of which are fortunately preserved in existing genera. We are therefore justified, when endeavouring to understand the mutual relationships of these families, in ignoring their more specialized genera. In other words, the relationships of families are the same as those of their more primitive genera. Unfortunately some families lack the primitive genera, which we may fairly assume once existed. We have no fossilized wings in this order, as in many other orders of insects, by which to test our assumptions. But we are not left wholly without resource. In the Lepidoptera (unlike the Trichoptera) the wing nervures (except the cross-veins) are developed in the pupal wings along the lines of the tracheae. We may therefore obtain great assistance from studies of the pupal tracheation and its gradual development into the structure of the imaginal wings. This line of research was originated by Comstock and Needham (1898-1899), and has been ably followed by Comstock (1918) and Tillyard (1919). Already it has given us help in difficult cases, and very much more help may be

confidently expected from it in the future. Unfortunately the study of the pupal wings of Lepidoptera has been much neglected. A profitable field of research lies before those who will master its technique and will have the patience to apply it in the study of cases in which the study of the adult wings leaves us at present in some uncertainty.

The importance of these preliminary remarks will become more evident as we proceed to examine the value of some neuration characters, which have been too much neglected in the classification of the Lepidoptera. I refer especially to the variations in the main trunks of the median and radial veins. A combination of the most primitive characters in the Cossidae is here illustrated (Figs. 2 and 3). In that family the median vein always persists, and there is almost always a strong vein within the cell running from the radial sector to the outer edge of the cell. This is the common stalk of the fourth and fifth radial veins, which, for reasons which will appear presently, I have called the *chorda* (Turner, 1918). In some of the genera of the Cossidae there is a tendency towards narrowing of the median cell in both wings, as in *Holocerus*, which may proceed so far as to cause its disappearance, as in *Stygia*, the primary branches having coalesced. Occasionally in the latter genus a small median cell may persist in the forewings. In the great bulk of the Heteroneura, however, these veins are totally absent, in others they are much reduced or vestigial. Yet they are always present, usually accompanied by the chorda, in the pupal wing, as was first discovered in the Rhopalocera (Comstock and Needham, 1898).

We will now pass to the Tineoidea, whose neuration is more primitive than that of many families, though less so than that of the Cossidae. Here all trace of the median trunk and the chorda are commonly absent, as in Figure 11. It will be noticed that here we have the neuration assumed to be primitive by Meyrick (Fig. 1). Actually this is a secondary condition due to asthenogenesis. That this is so is proved by the existence of these veins in a more or less attenuated condition in more than a few genera such as *Isotriasis* (Fig. 12) and *Cerostoma* (Fig. 13) (Turner, 1918). Finally, it has been found that they are present in the pupal wings of several genera (Tillyard, 1919) and undergo the same changes during the maturation of the wing as occur in the Rhopalocera. This obliteration of the basal median tracheal trunks affects the origin of the peripheral veins. M1 becomes approximated to R5, M3 to Cula, M2 is also frequently approximated towards the cubital, as in the Noctuoidea (Fig. 68), but it may retain its original position or become approximated to the radial as in the Geometroidea (Fig. 53); these changes resulting from these veins being captured by tracheae from the cubital or radial trunks (Tillyard, 1919). Similarly, in the hindwing, M2 may be attracted to the cubital as in the Noctuidae Quarifidae (Fig. 68) or remain in its original position, becoming obsolete through tracheal deprivation as in the Noctuidae Trifidae (Fig. 69); less often it is attracted to the radial in several families. These variations in the origin of M2, especially in the forewings, have been found of great service in classification.

The primitive areole in the forewings is persistent in some families, absent in others, and present in the more primitive genera of many. The methods of its disappearance vary. It is important to recognize that this disappearance may result from three different causes: (1) By obsolescence and loss of the chorda, the name which I have given to the lower limb of the radial fork, that is, the trunk of R4 and R5, which lies within the cell. I have already shown that this occurs in the Tineoidea. The lepidopterous cell after this obsolescence has been completed consists of both cell and areole, and I have called it an areocel (Fig. 14) (Turner, 1918). (2) By gradual approximation and eventual fusion of the chorda with the trunk of R2 and R3, which I have illustrated in the Cossidae (Fig. 15) (Turner, 1918). This process occurs in many groups. (3) The anastomosis of R2 with R3, that replaces the inter-radial cross-vein in the higher groups may be broken by dissociation, as occurs frequently in the Cymatophoridae, Oenochromidae, and the Sarrhothripinae subfamily of the Noctuidae, usually as an individual variation within the species.

#### THE PRIMARY DIVISIONS OF THE HETERONEURA.

##### *Asthenochorda and Sthenochorda.*

The classification which I propose is based primarily on the remarkable changes in the pupal wing discovered by Comstock and Needham (1898-9) in the Rhopalocera,

and by Tillyard (1919) in the Tineoidea, supported by my own observations on the imaginal wings of the latter group (1918). These concern (1) the loss of the median vein and its two primary branches, accompanied (2) by a similar obsolescence or disappearance of the chorda, which results in the merging of the primitive areole with the primitive lepidopterous cell to form what I have called an areocel (1918). All the superfamilies in which this occurs I have grouped into a Primary Division, to which I have given the name *Asthenochorda*. In this division the chorda has completely disappeared in the imaginal wing (though represented in the pupal neuration) in all except the Tineoidea. There it sometimes persists in a weak or vestigial condition, or very rarely as a fairly strong vein. This division includes the Rhopalocera, Zygaenoidea, Pyraloidea, Pterophoroidea and Tineoidea. Perhaps the inclusion of the Rhopalocera with these four superfamilies will come as a shock to some of my readers. But a little study should convince them that this proposal is not so revolutionary as may appear at first sight (Figs. 17 and 18). It is now many years since Meyrick (1895, p. 326) declared that the nearest allies of the Hesperidae are the Thyrididae. Long before this, the older conception that the Hesperidae were closely allied to the Castniidae was shown to be baseless by Westwood (1876, p. 157), who referred particularly to the primitive genera *Megathymus* (ibid., p. 205) and *Euschemon* (Pl. 29, f. 26).

The Rhopalocera, however, show some characters not found elsewhere in the *Asthenochorda*. They are:

(1). The presence of a humeral veinlet (or precostal spur) at the base of the hindwing. This appears to be always present except in the Lycaenidae and some genera of the Pieridae, which, presumably, have lost it.

(2). The loss of Cu<sub>2</sub> of the hindwing. In the Tineoidea this has been lost sometimes by asthenogenesis, but it is present in all the primitive genera of that group.

(3). The presence of R<sub>1</sub> in the hindwings of the Papilionidae and Elymnianae, running into the subcostal and so forming a precostal cell (Fig. 21).

(4). The presence of a cubito-anal cross-vein in the forewing in the Papilionidae (Fig. 20).

(5). The presence in the forewing of the Papilionidae of a second anal vein running into the dorsal margin (Fig. 20).

Of these, (2) and (3) are not uncommon in the *Sthenochorda*. A few of the *Sthenochorda* have precostal pseudoneuria but these appear to be recent adaptations, present or absent in closely allied genera, and not in my opinion homologous with the precostal spur of the Rhopalocera, among whom it appears to be a fundamental character. Character (4) is a unique development in the Heteroneura, but a similar cross-vein occurs in the Hepialidae. Whether this character has been directly derived from a common ancestor or has developed independently in the Papilionidae is doubtful. Character (5) is also unique in the Heteroneura, though an incomplete prolongation of A<sub>2</sub> beyond A<sub>1</sub> has been noted in a few genera.

In consequence of these differences, I propose to divide the *Asthenochorda* into two Subdivisions, the *Rhopalocera* and the *Microptila*.

For all the remaining Heteroneura I propose the name *Sthenochorda*. In them the chorda is always strong, but frequently fused with the radial sector and the common stalk of R<sub>2</sub> and R<sub>3</sub>, so that the areole disappears by coalescence. When this has happened, R<sub>3</sub> and R<sub>4</sub> are usually stalked. The "tortriciform neuration", characteristic of the most primitive genera of the *Microptila*, is never seen in this subdivision. There is no difficulty in following the steps by which the areole has disappeared in some genera of the Cossoidea and of the Drepanidae, Notodontidae, Geometroidea and Noctuoidea. To the *Sthenochorda* I refer also the Sphingoidea, Uranoidea, Bombycoidea, Lasiocampoidea and Psychoidea. In these the areole is never present in the adult wing, and R<sub>3</sub> is always stalked with R<sub>4</sub> (Fig. 16). Probably the areole may sometimes be found represented in the pupal wing, but Tillyard has shown that in *Doratifera* of the Psychoidea it has been eliminated by transference of R<sub>3</sub> to R<sub>4</sub> in the pupa, and so also in *Antheraea* of the Bombycoidea. In how many forms this has occurred we do not yet know.

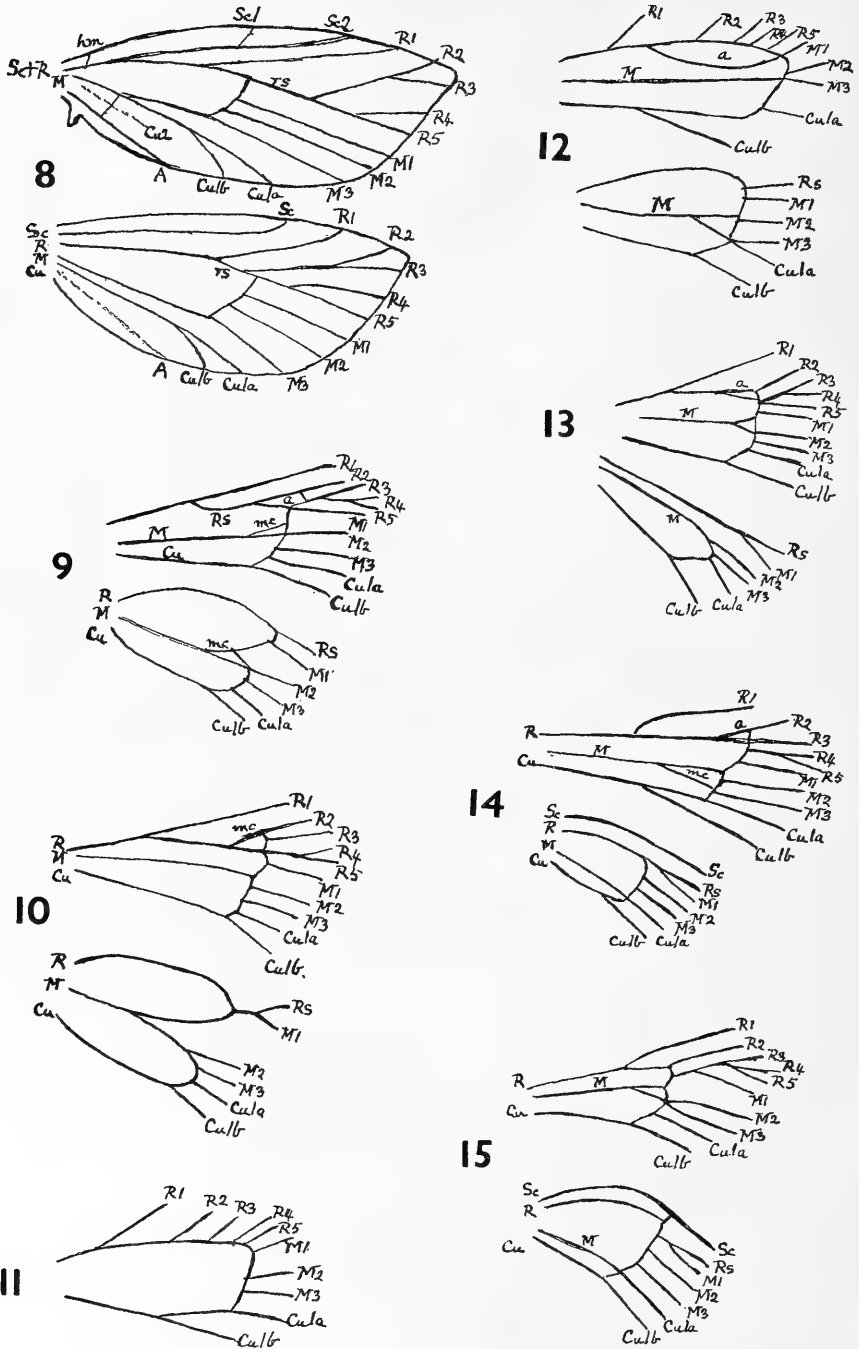


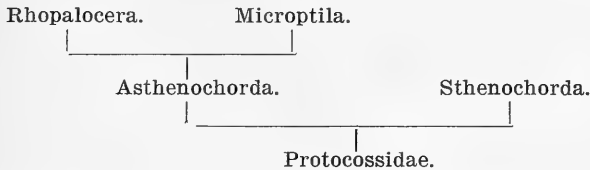
Fig. 8.—*Palaeoses scholastica* Turn. Figs. 9-15.—Diagrams of radial and median veins. Fig. 9.—*Holocerus nobilis* Stand. Fig. 10.—*Stygia australis* Latr. Fig. 11.—*Tortrix viridana* Lin. Fig. 12.—*Isotrias hybridana* Hb. Fig. 13.—*Cerostoma radiatella* Don. Fig. 14.—*Lentagenia tristani* Schaus. Fig. 15.—*Acyttara tigrata* Schaus.



Loss of the areole by dissociation occurs occasionally in the Sthenochorda, but never in the Asthenochorda. This loss, which occurs mostly when the areole is very long and narrow, is caused by the failure of the basal part of R3, which anastomoses with R4, to chitinize. In consequence R2 is stalked with R3, and R4 with R5, as in *Castulo* (Arctiidae) (Fig. 19).

It happens that, with the exception of the Zygaenoidea, whose affinities have not hitherto been rightly understood, the Microptila have long been known as an undefined group under the name of Microlepidoptera or "micros". Although this name has originated from the small size of the great majority of its species, size has never been regarded as its essential character. This has been so even in Europe, but in Australia it is still more evident. In this region many species of Geometroidea, Arctiidae, Nolidae and Noctuidae are much smaller than many species of the Xyloryctidae, Oecophoridae, Hyponomeutidae, Tineidae and other families of the Microptila.

The major divisions of the Heteroneura may be represented by the following diagram.



The Protocossidae is a hypothetical family conceived as combining the primitive cossid neuration (Fig. 2) with the five-jointed maxillary palpi of the Tineidae. Like the Hepialidae, members of this family were probably stem or root feeders and developed before the advent of flowering plants. They cannot, however, have developed from the Hepialidae, which is the termination of an early offshoot of the lepidopterous stem with rigid neurational characters. Their connection with the stem from which arose the Hepialoidea and Micropterygoidea, though real, must have been very remote.

#### SOME OBSERVATIONS ON NEURATION.

I propose to record here a few further observations, which are of importance in the classification of the Lepidoptera.

##### (1). *The Anal Veins of the Forewing.*

Originally there were three anal veins, but the third anal is preserved only in a few of the Homoneura. In *Sabatinea* alone of the Micropterygoidea is it present, the three anals forming a double loop (Fig. 4). In the Hepialidae it appears to be always absent, but in *Prototheora* it is present as a distinct vein running independently to the wing-margin (Fig. 6). A similar but weaker vein can be traced in *Anomoses* (Fig. 7). In the forewings of the Heteroneura there are never more than two, which arise from the base of the wing and unite to form a U-loop (3A having disappeared), as is shown in the accompanying figures, which illustrate also the steps by which it becomes replaced by a single vein. In the Pyraustidae the loop, when present, has a characteristic boat-shape (Fig. 33). Simplification in the majority of cases is accomplished by the obsolescence of the lower limb (A2) of the loop (Fig. 24). Only in one genus, *Endrosis*, have I so far observed obsolescence of the upper limb (1A); and in none have I seen a coalescence of the two limbs. In *Synemon*, in *Cerura*, and in two genera of Noctuidae (Figs. 26 and 51), I have observed a prolongation of 2A beyond the loop comparable to that in the Papilionidae, though less marked (Fig. 25).

##### (2). *The Anal Veins of the Hindwing.*

Three anal veins are present in the more primitive Homoneura and Heteroneura (Fig. 25). Tillyard has shown (1919) that in the pupal tracheation of the most primitive genera of both groups 1A runs very close to, or actually fuses with, Cu2 near its base, then separates and approaches 2A. In the imaginal wing scarcely a trace of this course remains. 1A and 2A fuse, leaving a small V-loop at their base. By reduction this loop tends to disappear in many cases as does 3A.

(3). *The First Radial and Subcostal of the Hindwing.*

What is commonly called the subcostal in the Heteroneura is really a compound vein Sc + R1 (Fig. 21*b*). In the more primitive genera of many families R1 runs into Sc to form this compound vein. In others R1 disappears, being completely fused with Sc from near the base of the wing (Figs. 28 and 67). An important aid is given to phylogeny and classification by these changes.

(4). *The Second Cubital Vein.*

This is normally a weak vein in both wings, and it shows a strong tendency to become obsolescent or absent. In the Hepialoidea (Fig. 5) it is normally developed in the hindwing, but is weakly developed from the base in the forewing, and disappears altogether before half its normal course is run. In the Rhopalocera it is always absent in both wings (Fig. 20). In the Tineoidea it is absent or vestigial in the forewing, only its terminal end being, in some, developed for a short distance (Fig. 36); but is normally or weakly developed in the hindwing. In the Pyraloidea (Fig. 33) it is absent, or rarely vestigial, in the forewing; in the hindwing it is normally developed or weak. In the Pterophoroidea (Figs. 34 and 35), on the contrary, it is normally developed in both wings, as also in the Zygaenoidea (Figs. 29 and 30).

In the taxonomy of the Sthenochorda the variations in Cu2 are important. In the Cossioidea it is normally developed in both wings in the Cossidae (Fig. 2) but in the hindwing only in the Arbelidae and Argyrotylidae. In the Castnioidea it may be developed in the forewing only (Figs. 92-94). In the Psychoidea it is present in both wings (Figs. 89 and 90). In the more primitive genera of the Tineoidea its apical portion only is developed in the forewing, but the whole vein in the hindwing.

(5). *The Second Median Vein.*

I have heard the objection raised, that neuriation is an unsatisfactory guide to classification, because it is so often variable. The fact alleged is correct; the deduction is fallacious. It reflects an *a priori* attitude and a want of observation. Some details of neuriation, for instance, the approximation, stalking, or even the coalescence of certain veins, may occur within the limits of a species; that of others may give good generic characters, others again are characteristic of whole families or even superfamilies. Only by careful study can we learn their relative importance. There is another *a priori* assumption that has proved misleading to some. This is the supposition that a character that has proved valuable in one group will necessarily prove of equal value in another group. Nature has no respect for this assumption. For instance, the stalking or coalescence of R4 and R5 of the forewing is a family character in the Oecophoridae, but is not always of generic value in the Hyponomeutidae and Glyphipterygidae. Again, the coalescence of these veins is a useful generic character in the Oecophoridae, but in rare instances occurs as an individual abnormality in a genus, in which these veins are normally stalked. It would be possible, but is not necessary, to give other similar instances.

Experience has shown that variations in the origin of M2 of the forewings are of much higher value than changes in other peripheral veins. For this we can see a reason. These variations arise from the loss in the pupal wing of the tracheae, on which are formed the median veins within the cell. As a consequence M2 in the pupal wing may be captured by a tracheal branch arising from Cu1*a*, with the result that in the imaginal wing M2 becomes approximated in origin to M3 (Tillyard, 1919). This does not always occur; M2 may retain its original position, or may become approximated to M1; for M1 is captured by a tracheal branch from R5, and this sometimes captures M2 also.

In the hindwing M2 may remain in its original position either fully developed or, as a result of diminished tracheal supply, weakly developed or obsolescent or completely absent. On the other hand, owing to capture of its trachea by the cubital, its origin may be more or less approximated to M3, in which case the vein remains fully developed. This is well illustrated in the Noctuidae by the differences between the hindwings of the Trifidae and the Quadrifidae (Fig. 69). Much less commonly M2 moves in the opposite

direction, its origin becoming approximated to that of M1. These differences are valuable as characters for the definition of genera, and sometimes of subfamilies or families, but carry less weight than the corresponding variations in M2 of the forewing.

In the Rhopalocera, M2 is inconstant in position; it does not, as in the other two divisions of the Heteroneura, give us any guide in the discrimination of families. In the Hesperidae the subfamily Pamphilinae has this vein approximated to M3, whereas in the other subfamilies it arises midway between M1 and M3 (Fig. 28).

In the Microptila, the Zygaenoidea have M2 always approximated to M3 in the forewing, but only occasionally in the hindwing (Fig. 29). The Pyralioidea have M2 approximated to M3 in both wings, except in the Tineoidea and the genus *Addaea* (Thyrididae). In the forewing these veins may be stalked or coincident. In the Pterophoroidea the primitive genus *Agdistis* shows the same approximation in the forewing, but in the hindwing these veins are coincident (Fig. 34). In the cleft-winged genera the relations of these veins are obscured (Fig. 35). In the Tineoidea, after excluding those that have undergone extreme reduction of veins, M2 is usually approximated to M3 in both wings, but there are many exceptions, in which it arises from the midway position in one or both wings.

In the Sthenochorda the variations in M2 of the forewing are of much value in distinguishing superfamilies. It is approximated to M3 in the Cossioidea, Castnioidea, Psychoidea, Lasiocampoidea, Drepanoidea and Noctuoidea. This approximation is always distinct but varies in degree. For instance, in the Cossidae the most primitive genera have these veins moderately but not closely approximated, but in most of this family the approximation is more pronounced, and rarely may result in these veins becoming connate. In the higher groups the approximation is sometimes replaced by stalking or coalescence.

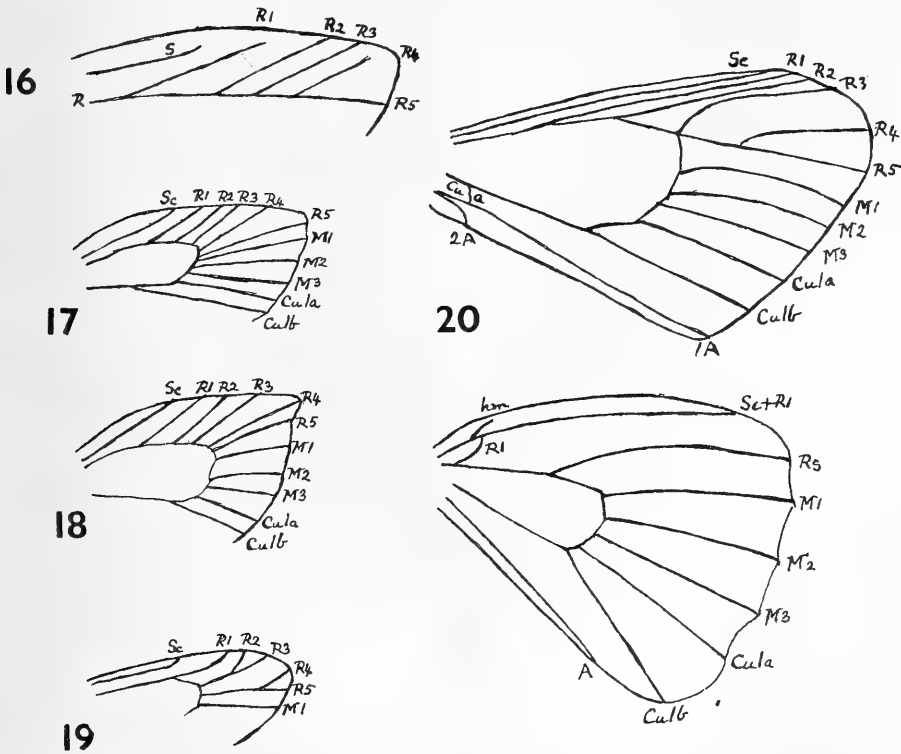


Fig. 16.—*Doratifera vulnerans* Lewin. Part of pupal forewing showing transference of R3 to stalk of R4 and R5 (Tillyard). Fig. 17.—*Hesperia tages* Lin. Fig. 18.—*Striglina scitaria* Wlk. Fig. 19.—*Castula doubledayi* Newm. Fig. 20.—*Papilio aegeus* Don. cula., Cubito-anal cross-vein.

On the other hand, M2 arises from midway between M1 and M3 or is approximated to M1 in the Bombycoidea, Sphingoidea, Uranoidea, and Geometroidea (except in the genus *Microdes* of the Larentiadae).

#### A GENERAL SURVEY.

Having completed our examination of various details of neuriation, let us now stand back and take a general view of the position attained. We commenced by dividing the Lepidoptera into two suborders of very unequal size, the Homoneura and Heteroneura. This division, we believe, is now generally accepted. We divided the latter into two divisions, the Asthenochorda and Sthenochorda. This is a new conception, but appears securely based on two different lines of evolution. The distinction between them is clear and unambiguous, though the primitive representatives of both are derivable from a common stem, for which I have proposed the name Protocossidae, denoting a hypothetical family combining the primitive neuriation of the Cossidae with the primitive mouth-parts of the earliest Tineoidea. We then considered more in detail the position of the Rhopalocera. It was evident that though these appeared more nearly allied to the other superfamilies of the Asthenochorda than to the Sthenochorda, they differed from the former in some important characters, which appeared amply sufficient to justify their separation as a distinct subdivision. We found no sufficient reason to exclude the Hesperidae from the Rhopalocera, though it forms a very distinct superfamily, specialized in some respects, but more primitive in others. It now remains to make a more detailed examination of the families and superfamilies. As to the former there appears to be (with a few exceptions) general agreement; but as to the latter no such agreement has yet been obtained. In the classification here proposed the superfamilies are based on structural characters and differ much in extent. Many of them consist of a single family. Others are dominant groups and contain many families.

#### THE SUPERFAMILIES OF THE RHOPALOCERA.

From all the other Rhopalocera the Hesperidae differ in their simple tortriciform neuriation (Fig. 17), their broad head, and usually their peculiar hooked antennae. To this may be added the usual presence of middle spurs in the posterior tibiae, the presence of a frenulum and retinaculum in *Euschemon* (Fig. 28), and the curious backward direction of the humeral veinlet in the hindwing, which occurs also in *Eurycus* of the Papilionidae (Figs. 22 and 23). Taking all these characters together, with special stress on the first, I agree with Meyrick in admitting the superfamily Hesperoidea, but I think he goes too far in writing (1927) that they have no connection with the rest of the Rhopalocera, "the resemblance being in part analogical and the differences profound". On the contrary, the stalking of R3 and R4 of the forewings, which is present in all the latter, appears to be strictly analogous to their stalking in the great majority of the Pyraloidea. There is a very strong probability that, as in that superfamily, the stalking is a modification of a previous tortriciform condition. If this be admitted there seems to be no reason to consider the Hesperoidea as other than a specialized offshoot from the primitive rhopalocerous stem.

I divide the remaining families into the Papilionoidea and Nymphaloidea. The former shows the following peculiarities: (1) There is a cubito-anal cross-vein in the forewings (Fig. 20). (2) The vein 2A in the forewings runs independently to the dorsal margin. (3) The subcostal and first radial arise independently from the base of the hindwings and fuse to form a precostal cell. (4) One anal vein has been lost in the hindwings. Three of these characters are peculiar to the Papilionidae; the third is, so far as I know, present also only in the genus *Elymnias* of the Nymphalidae, and not elsewhere in the Asthenochorda, though it is found in several groups of the Sthenochorda.

Of the Nymphaloidea three families are contained in the European and Australian faunas, the Lycaenidae, Pieridae and Nymphalidae. The first two present some similarity, but it is doubtful whether this is not due merely to convergence. It is certainly remarkable that the Pieridae and Papilionidae, so different in the imago, are so similar in their pupae. In these two families the angular pupa, girdled with a silken thread and with head uppermost, is a fixed character. The suspension with the head

downwards without a girdle in the Nymphalidae may, I think, be a later development from this. It is difficult to see how the nymphalid position could have been changed into that of the Pieridae and Papilionidae, but the contrary change is not difficult to understand. In neurational characters the Lycaenidae, which have lost the precostal spur in the hindwing, and usually one vein of the forewing, are probably the most recent. This is confirmed by their small size (an instance of the asthenogenesis so operative in the Lepidoptera), their present dominance in number of species, and the intimate association of many species with ants.

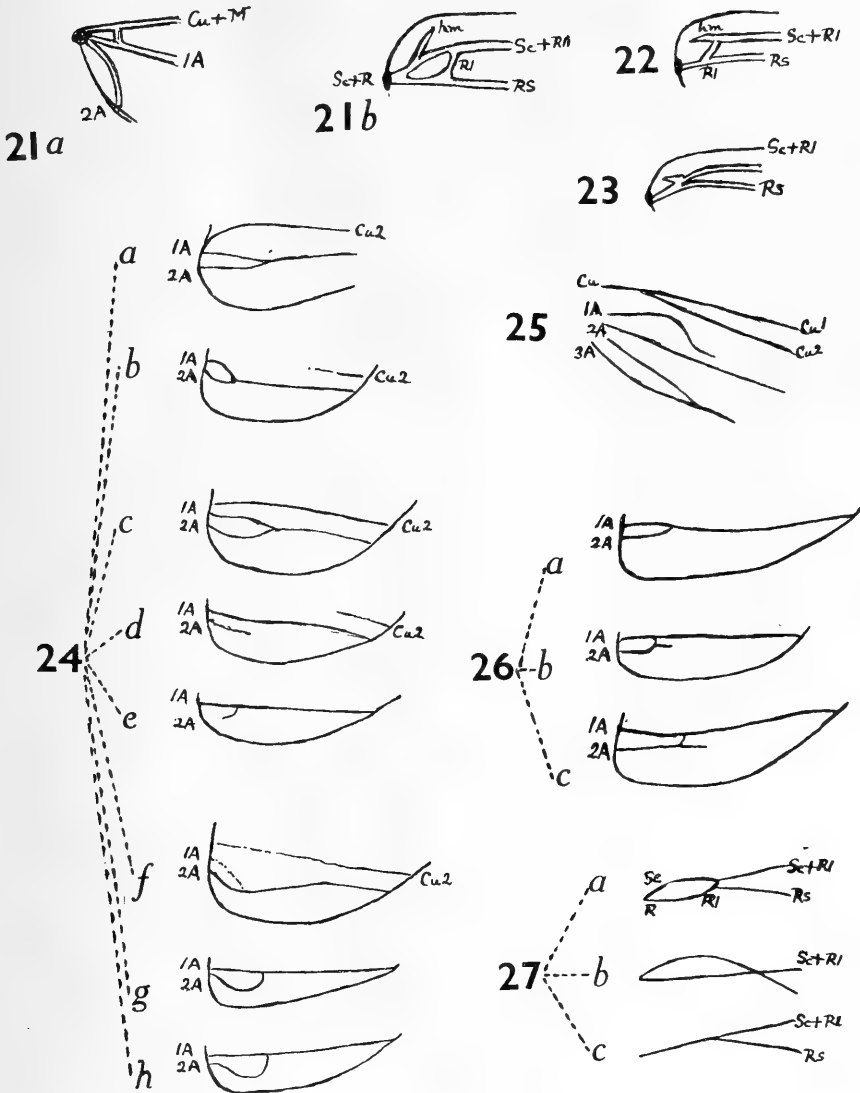


Fig. 21a.—*Papilio aegaeus*. Parts of bases of fore- and hindwings. Figs. 21b-23.—Part of base of hindwings. Fig. 21b.—*Papilio aegaeus*. Fig. 22.—*Eurycyus cressida* Fab. Fig. 23.—*Hasora haslia* Swin. Fig. 24.—Anal veins of hindwings. a. *Macrocyttara expressa* Luc. b. *Tortrix musculana* Hb. c. *Carcina quercana* Fab. d. *Monopis rusticella* Hb. e. *Tinea corticella* Curt. f. *Endrosis lacteella* Schiff. Fig. 25.—*Laspeyresia pomonella* Lin. Pupal tracheation of part of hindwing (Tillyard). Fig. 26.—Anal veins of hindwings. a. *Biston betularius* Lin. c. *Othreis materna* Lin. Fig. 27.—Subcostal and radial veins of hindwings. a. *Stilpnotia salicis* Lin. b. *Porthesia chrysorrhoea* Lin. c. *Tyria jacobaeae* Lin.

## THE SUPERFAMILIES OF THE MICROPTILA.

## SUPERFAMILY ZYGAENOIDEA.

This was probably at one time a much more extensive group than it is at present, and is now represented by fragments only of its former extent. There is no trace of a chorda in the imaginal wing, but a median vein is present in both wings, usually a single vein, rarely forked in the forewing, still more rarely in the hindwing. Figure 29 shows a primitive tortriciform neuration; Figure 30 is a more specialized form with stalking of the forewing radials, together with stalking of M2 and M3 in the forewing, but is more primitive in having intracellular forked medians. In this family, Cu2 is present in both wings, and in the hindwing R1 arises from the middle, or beyond the middle, of the cell and is very short, the subcostal being closely approximated to the cell. In some instances this short vein is replaced by an anastomosis.

## SUPERFAMILY PYRALIDOIDEA.

This large and well-characterized superfamily is one of the dominant groups of the Lepidoptera. It contains six families, which have been clearly defined by Meyrick and Hampson. The tortriciform neuration, which has been shown to be characteristic of the Asthenochorda, occurs in most of the Thyrididae (Fig. 18) and in one genus of the Pyraustidae. No trace of the chorda or median is present in the imaginal forewing, but Tillyard found that they were present in the pupal forewing of *Morova*, the New Zealand representative of the Thyrididae. In the great majority, R3 and R4 of the forewing are stalked, but sometimes coincident in the Phycitidae. M2 is approximated to M3 in both wings. Cu2 is absent in the forewing but, except in the Thyrididae, present in the hindwing, which has two anal veins, one being the conjoint 1A + 2A, the other 3A. A distinctive character is the approximation or anastomosis of the radial sector to the subcostal beyond the cell of the hindwing. The former occurs in the Thyrididae and some genera of the Pyralidae; but in all other cases these veins anastomose almost immediately after the origin of the radial sector. Except in the Thyrididae and a section of the Pyralidae, the maxillary palpi are sufficiently developed to be easily recognizable.

As a representative I figure one of the Pyraustidae (Fig. 33). The boat-shaped loop formed by 2A in the forewing is well shown. This appears to be peculiar to that family, but in most of its genera 2A has disappeared. A simple anal is the rule in the other families; a small basal V-loop is rarely present. The anastomosis of S and Rs in the hindwing is characteristic. The more primitive condition, in which these veins are merely approximated, is shown in Figures 31 and 32.

The Tineodidae is a small family related to extinct forms of Pyraustidae, from which the family differs in M2 of the hindwing arising from the middle of the cell well separate from M3 (only in *Tanycnema* are these veins somewhat approximated); M1 may be either connate or separate from Rs, which is either approximated to, or anastomoses with, S beyond the cell. In the forewing all veins from the cell may be separate or R3 and R4 may be stalked. Except in *Tanycnema* the maxillary palpi are distinct. *Oxychirota* is an anomalous genus with extremely narrow wings, R2, R3, R4 and R5 being stalked. *Coenoloba* is unique in having both wings 2-cleft. The forewing has Cu1a and Cu1b stalked; and R1, R2, R3 and R4 stalked; the hindwing Cu1a and Cu1b stalked, M1 and Rs stalked; and Rs anastomosing with the subcostal. The maxillary palpi are rather large and triangularly scaled.

The small number of existing genera (all but one Australian) so far known, together with their extraordinary diversity, points to this being an archaic group, which has suffered much extinction, leaving only a few survivors.

## SUPERFAMILY PTEROPHOBOIDEA.

This group is remarkable for the extensive fissuring usual in both wings. In the forewing the Pterophoridae are 2-cleft (rarely three- or four-cleft), in the hindwing usually 3-cleft. Fortunately there are three genera in which the wings are not cleft, and these are the best guide for the phylogeny. In *Agdistis* (Fig. 34) the neuration of the forewing is archaic, all the veins from the cell of the forewing arise separately, while

Cu2 is developed in both wings. The fusion of M2 and M3 of the hindwings is a specialization. The presence of Cu2 in both wings seems to be an invariable character in the Pterophoridae, and R3 and R4 may be stalked or coincident (Fig. 45). In some genera, such as *Alucita*, the neuration is much reduced. The maxillary palpi are always obsolete. A curious character is the presence of a double row of short spine-like dark scales on the lower margin of the cell beneath. There is probably real but rather remote affinity between the Pterophoridae and the Tineoidea.

In his Revised Handbook, Meyrick removed the Orneodidae to the Tineoidea, but later he restored them to the place they occupied in his first Handbook, immediately

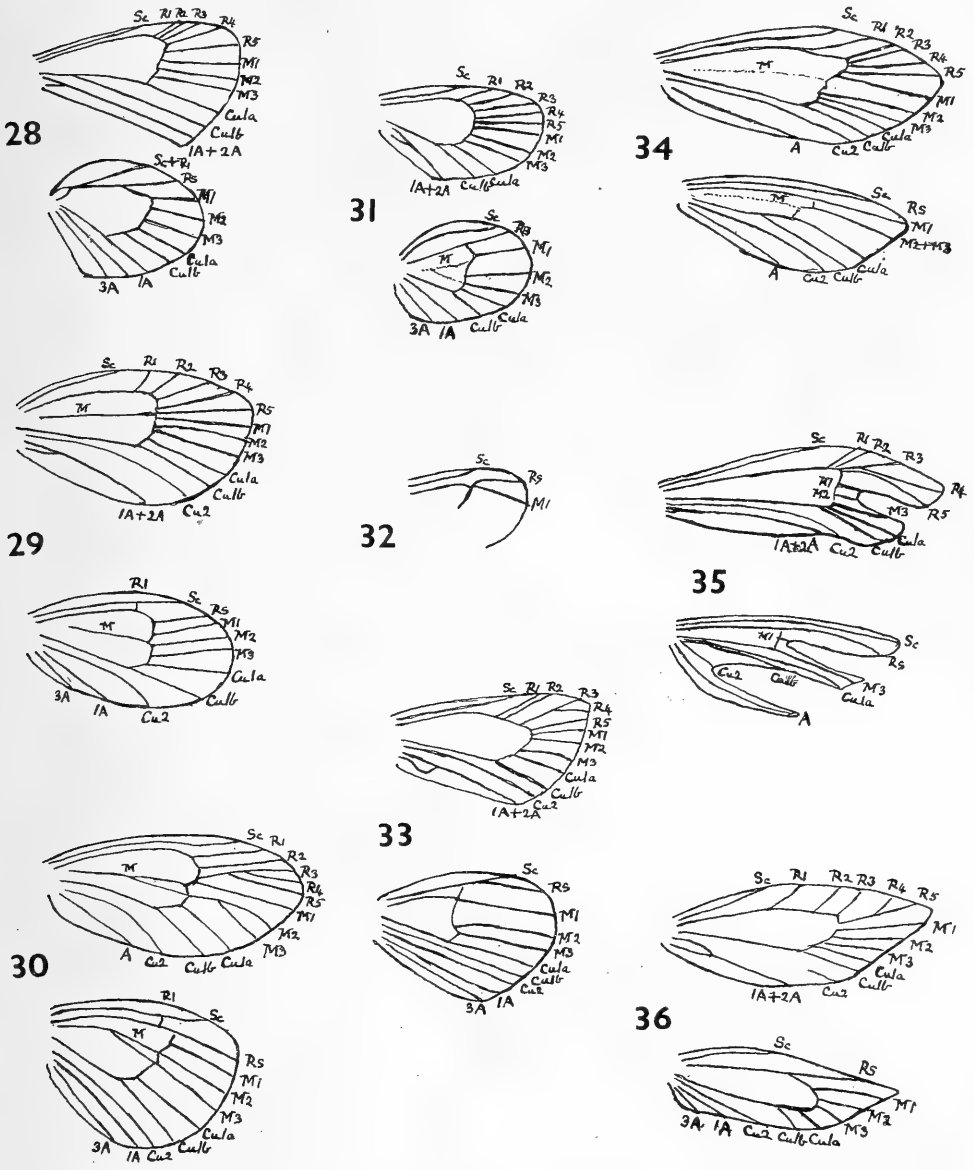


Fig. 28.—*Euschemon rafflesia* Macl. Fig. 29.—*Procris statices* Lin. Fig. 30.—*Chelura bifasciata* Hmps. (after Hampson). Fig. 31.—*Striglina irias* Meyr. Fig. 32.—*Epipaschia atribasalis* Warr. Part of hindwing. Fig. 33.—*Mecyna ornithopteralis* Gn. Fig. 34.—*Agdistis benetti* Curt. (after Meyrick). Fig. 35.—*Stenoptilia pterodactyla* Lin. (after Meyrick). Fig. 36.—*Mompha fulvescens* Haw. (after Meyrick).

following the Pterophoridae. They are a small group of four genera, three of which have both wings 6-cleft; the other has the forewing 6-cleft and the hindwing 7-cleft. In *Orneodes* the wings are fissured nearly to the base and each segment is occupied by a single vein.

The superfamily Pterophoroidea does not have Rs of the hindwing more closely approximated to the subcostal beyond the end than before the end of the cell. It also differs from the Pyraloidea by the presence of Cu2 in the forewing.

#### SUPERFAMILY TINEOIDEA.

This immense superfamily comprises more than one-third of the known Lepidoptera, and when the world fauna is better known should approach one-half. It contains the most primitive of the Heteroneura, for its only rival, the superfamily Cossoidea, is less primitive in its mouth-parts. Among the primitive characters that it occasionally presents are (1) the 5-jointed folded maxillary palpi; (2) the occasional presence of the chorda, seldom strongly developed, in the forewing (Figs. 12 and 13); (3) occasionally a weak or vestigial median, seldom forked, in the cell of both wings; (4) the second cubital more or less developed in both wings; (5) the first and second anals forming a basal loop in both wings; and (6) the third anal in the hindwings. These characters are rarely combined in one genus. The long folded maxillary palpi are found only in the Nepticulidae and the Tineidae (*sensu lato*), but in many of the latter family they are short or absent. The chorda and median veins in the cell have disappeared in the great majority of the genera, and the resultant tortriciform neuriation has been lost in a great many by stalking. It is noteworthy that the first radial veins to be stalked are almost always R4 and R5, not R3 and R4 as in the preceding superfamilies.

These changes in neuriation are small compared with those that have occurred in a great number of genera, which have undergone asthenogenesis to such an extent that it is sometimes difficult to recognize which veins have been retained. From this aspect the Tineoidea contains some of the most specialized of the Lepidoptera, small, narrow-winged, and often minute. In the accompanying figures (Figs. 40-46) it will be observed that, except in *Opostega* (Fig. 45), the forewings have their neuriation relatively slightly reduced. The hindwings have undergone greater reduction, the loss affecting mostly the median veins. Cu2 has been lost in some; one has lost a branch of the first cubital; but all have retained 1A and 3A.

I can see no justification for the separation of the Tortricoidea as a separate superfamily. This opinion was expressed many years back by Walsingham. Meyrick himself states in his Revised Handbook (p. 25) that "the Tortricina originated from the Glyphipterygidae, the Eucosmidae being the basic family, and its most primitive genus, *Laspeyresia* (with its allies), approaches certain special forms of the Glyphipterygidae in all structural and superficial respects so closely, that it is difficult to draw any line between them".

Not only is the Tineoidea the most dominant superfamily of the Lepidoptera at the present time, but it appears still to be undergoing active evolution. The number of known species is overwhelming, and is being increased every year, while in many regions this part of their fauna has hitherto hardly been touched. At the date of the publication of the Revised Handbook, Meyrick recognized 33 families, of which 21 were British, in his Tineina (excluding the Tortricina). These he divided into seven "tribes" with names ending in -oidea. As this suffix has been generally used by entomologists to denote superfamilies, this usage appears inadmissible, and some other form of nomenclature seems to be needed. The immense amount of work done by Meyrick in this group, and his great experience, should make us very careful in making any change in his classification. His nomenclature may, I think, be varied by regarding his "tribes" as families and his families as subfamilies. For instance, the Tortricidae may be divided into Phalonianae, Tortricinae, Eucosminae, etc., and the Gelechiadae into Gelechianae, Oecophorinae, etc. I doubt whether all his groups are equally valid, but I shall propose only one major alteration. Meyrick regarded the Cosmopterygidae as developed by asthenogenesis in his Gelechioidea, the Elachistidae, Douglasiadae and S ythidae in his Hyponomeutoidea, and the Coleophoridae in his Plutelloidea.



Convergence through asthenogenesis is common in the Lepidoptera, and his judgment may be correct. But he seems to me to fail in this instance to give clear reasons for this decision. In view of the close correspondence in neuration and other characters of these five groups, I propose, but with some diffidence, to consider them as subfamilies of the Elachistidae.

The following list, which includes only groups represented in the British and Australian faunas, includes 9 families and 30 subfamilies.

1. Elachistidae with the five families already mentioned.

2. Gelechiadae with seven subfamilies, Gelechianae, Xyloryctinae, Blastobasinae, Oecophorinae, Thalamarchellinae, Amphitherinae and Hyponomeutinae.

This is a very extensive group; the Gelechianae containing over 3,500 and the Oecophorinae over 3,000 known species. On the other hand, only 8 of the Amphitherinae and 4 of the Thalamarchellinae have been described. This great disparity does not invalidate the status of these groups, which is not concerned with the number of species in each group, but with the conception of the evolutionary stems, as deduced from structural characters, on which they have developed. Furthermore, the affinities of these stems depend entirely on their most primitive genera, and are in no way affected by their specialized genera, however far these may have diverged.

3. Tortricidae with four subfamilies, Phaloniana, Tortricinae, Eucosminae and Chlidanotinae.

All these are closely allied, especially the second and third, which are separated by only one character, not of great morphological value and not absolutely constant.

4. Copromorphidae with two subfamilies, Carposininae and Copromorphinae.

5. Aegeriadae.

6. Glyphipterygidae with three subfamilies, Heliozelinae, Heliodininae and Glyphipteryginae.

I am somewhat doubtful about the position of the first two subfamilies.

7. Plutellidae with three subfamilies, Gracilariana, Epermeniana and Plutellinae.

8. Nepticulidae.

As Meyrick points out, the neuration of this family is peculiar in the absence of the cell in both wings. In the forewing this is associated with a basal coalescence of the median with either the radial or cubital or both (Fig. 47). This is a structure not found elsewhere in the Lepidoptera, and Meyrick has suggested that the family arose by a separate stem from the Micropterygoidea. This seems to me unlikely. The family Nepticulidae has a normal frenulum, and the palpi conform to the tineoid type. I think it is probable that it is an ancient offshoot from the Tineidae, and is not entitled to more than family status.

9. Tineidae with seven subfamilies, Epipyropinae, Cyclotorninae, Oposteginae, Lyonetiana, Tineinae, Lamproniana and Adelinea.

This group, together with the Nepticulidae, contains all the Heteroneura, which have retained the primitive long five-jointed folded maxillary palpi. It includes also many in which the maxillary palpi are short or absent. The Epipyropinae and Cyclotorninae are small groups whose larvae have become specialized in their habits. In both, the neuration is of primitive tineoid character. The former have lost maxillary and labial palpi and tibial spurs; and their larvae are parasitic on Homoptera. The latter have lost maxillary palpi, their labial palpi are very short, straight, stout and obtuse, but the tibial spurs are well developed; the larvae spend their later stages in ants' nests. The Oposteginae, with their extremely degraded neuration, not explicable by mere reduction in size, appear to me to be more entitled to subfamily rank than many recognized subfamilies. Compare the neuration of *Opostega* (Fig. 45) with that of *Leucoptera* (Fig. 46).

#### THE SUPERFAMILIES OF THE STENOCHORDA.

##### SUPERFAMILY BOMBYCOIDEA.

Tongue, palpi and frenulum present or absent. No median vein in cell of both wings. Forewings without areole except in Cymatophoridae and Notodontidae; R3, R4

and R5 usually stalked, M2 from middle or above middle of cell, Cu2 absent (except sometimes in Bombycidae). Hindwings with Cu2 and A3 present or absent.

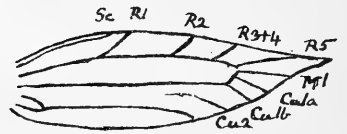
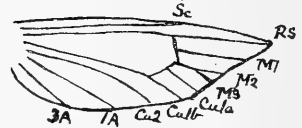
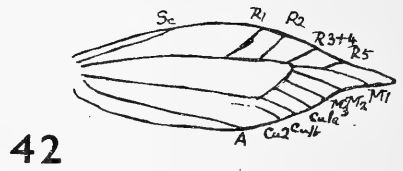
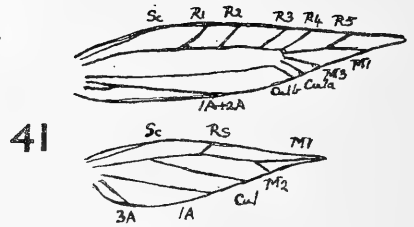
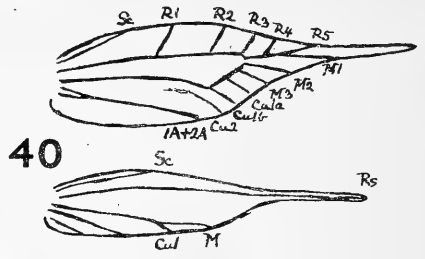
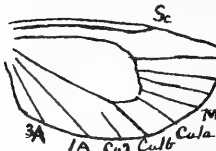
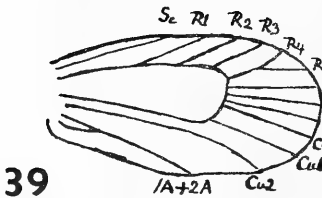
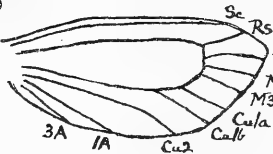
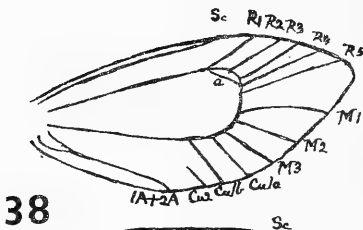
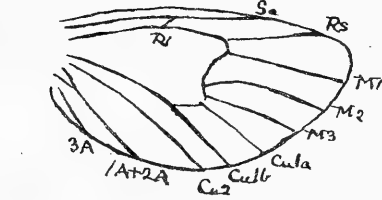
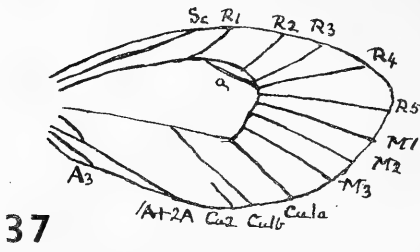


Fig. 37.—*Argyroproce salicella* Lin. Fig. 38.—*Moerarchis australasiella* Don. Fig. 39.—*Thalamarchella alveola* Feld. Fig. 40.—*Cosmopteryx druryella* Zel. (after Meyrick). Fig. 41.—*Douglasia ocerostomella* Stn. (after Meyrick). Fig. 42.—*Seythris fuscoaenaea* Haw. (after Meyrick). Fig. 43.—*Coleophora onosmella* Brahm. (after Meyrick).

There are six families, which form a natural group, though with some diversity of structure. For instance, the frenulum is absent in the Saturniadae and Brahmaeidae, present in the Cymatophoridae and Notodontidae, while in the Bombycidae it may be present or absent. Though the presence or absence of the frenulum is usually a family character, too much weight has been given to it. In the Geometridae every stage between a well-developed, weakly-developed and absent frenulum is found within a very clearly defined family, and *Euschemon* must be placed in the Hesperidae, in spite of its strong frenulum in the male.

The family Saturniadae is the most specialized and is remarkable for the combination of large size with reduced neurulation. Tillyard's examination of the pupal wing of *Antheraea* showed that even in that stage there was no areole, also that in the forewing the radial was four-branched and the median two-branched. The tongue and frenulum are absent. The palpi are short or obsolete, and the same applies to the tibial spurs. Middle spurs on the posterior tibiae are never developed. The forewings have no areole, M2 is absent, R2 and R3 are coincident. In the hindwings the subcostal diverges widely from Rs. R1 is absent, Rs arises much before the angle of the cell, and Cu2 is absent. In *Attocus* the discocellulars are absent leaving the cell open in both wings (Fig. 48).

In this family I include the genera, which have been known as Citheroniadae. The Saturniadae includes some of the largest of the Lepidoptera, an order in which size, unless compensated by some other factor, is a hindrance to survival. The family appears to have become over-specialized, and as a consequence, the species are not numerous, probably less so now than in the more or less remote past. These remarks apply also to the Brahmaeidae, and to a less degree to the other three families.

In the Bombycidae (in which I include the Eupterotidae) the tongue is absent; the palpi short or obsolete; the frenulum present or absent (in *Bombyx* it is rudimentary). In the forewing R2, R3, R4 and R5 are stalked or R2 is absent, Cu2 is rarely present, and there is no areole. In the hindwing the subcostal diverges from the cell near the base, 3A is present, but Cu2 is rarely developed (Figs. 49 and 50).

The Brahmaeidae (Hampson, 1892) consists of only one genus and a few species in the Oriental region. The tongue is present. The palpi large rounded and upturned. The frenulum absent. In the forewing M2 arises from the upper angle of the cell. In the hindwing the subcostal is approximated to the radial sector beyond the cell, which is short, M2 arises from near the upper angle of the cell, 3A is absent and Cu2 is absent in both wings.

In the Cymatophoridae tongue and frenulum are present. In the forewing there is a long, narrow areole, which may be present or lost by dissociation within the same species. In the hindwing Rs arises before the angle and is curved and approximated to the subcostal beyond the cell, 3A is present in the hindwing, but Cu2 is absent in both wings.

In the Notodontidae the tongue may be present or absent. The frenulum is present. The forewing may or may not have an areole. In the hindwing the subcostal is usually approximated to the cell, M2 is weakly developed or seldom absent and 3A is present. This is the most primitive of the six families. There are two subfamilies. The Cnethocampinae represents an early offshoot from the notodontid stem, differing from the Notodontinae by the tongue being always absent, the palpi being small or obsolete, the abdomen having a large apical tuft, and the hindwings with the subcostal sometimes widely separate from the cell, but more often approximated at one-fourth and sometimes further (Fig. 52). In the Notodontinae the tongue may be well developed, weakly developed, or absent; the palpi are always present; and the subcostal of the hindwing is usually approximated to the cell to near its end, always to its middle, rarely connected or anastomosing (Fig. 51).

#### SUPERFAMILY GEOMETROIDEA.

Tongue usually well developed. Frenulum present except in some Geometridae. Forewing often with areole, but no median in cell of either wing; R1 often anastomosing with R2, R4 and R5 stalked, R3 often stalked with them, Cu2 absent, M2 from middle or

above middle of cell. Hindwing with Sc bent at base into a humeral angle, Cu2 absent, 3A present or absent. In *Microdes* (Larentiadae) M2 of forewing arises below middle.

This is a large and dominant superfamily in the Sthenochorda, second only to the Noctuoidea. It contains five families, the Larentiadae, Sterrhidae, Geometridae, Boarmiadae and Oenochromidae. The distinctions between the families have been so

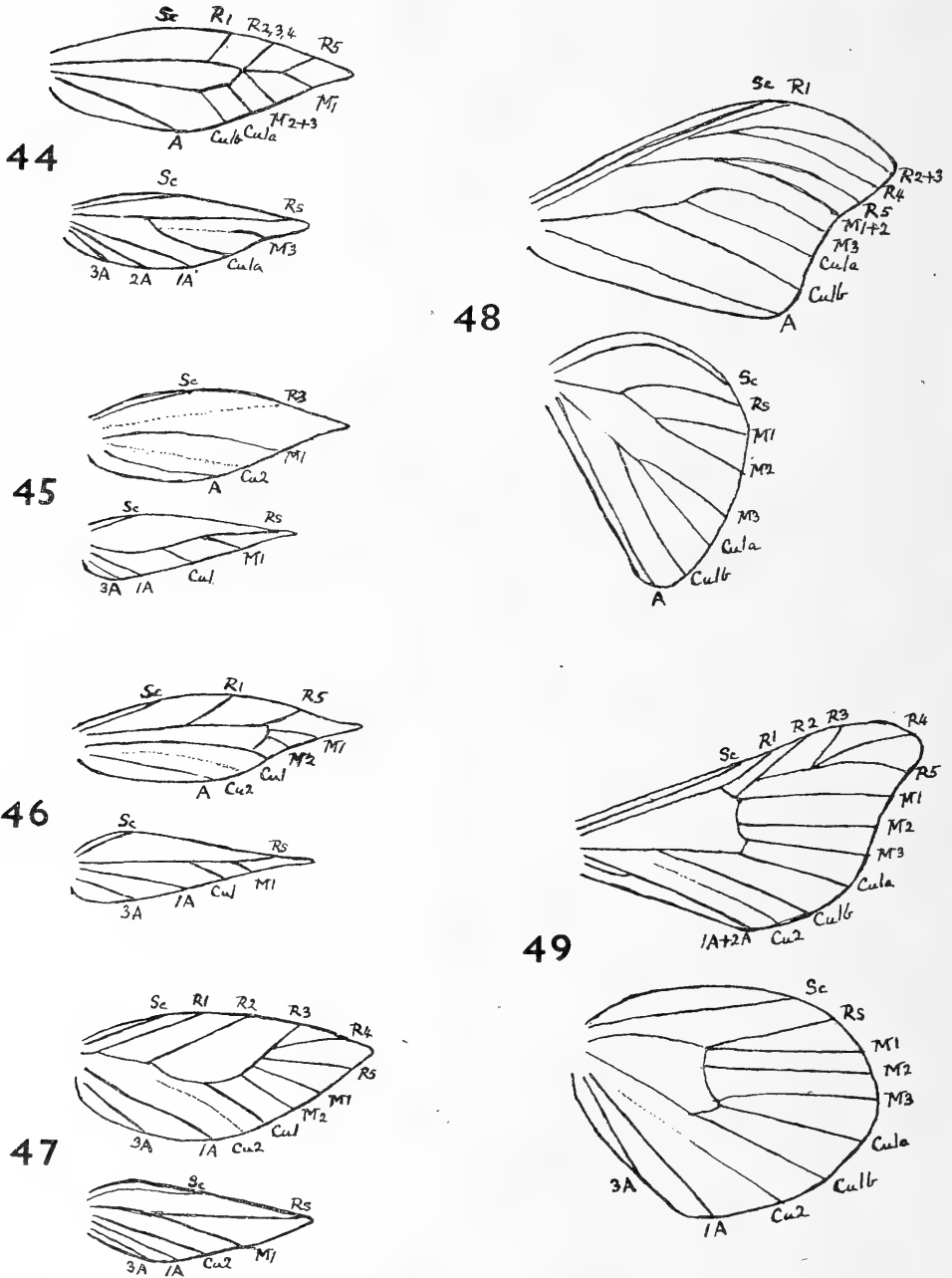


Fig. 44.—*Heliozela stannella* F.v.R. (after Meyrick). Fig. 45.—*Opostega crepusculella* Zel. (after Meyrick). Fig. 46.—*Leucoptera laburnella* Stn. (after Meyrick). Fig. 47.—*Scoliaula quadrimaculella* Boh. (after Meyrick). Fig. 48.—*Attacus dohertyi* Roths. Fig. 49.—*Bombyx mori* Lin. (after Comstock).

well given by Meyrick and Prout that it is not necessary to recapitulate them here. The first four are clearly defined; the Oenochromidae are fewer in species, but show more variation in structure, varying from primitive to specialized forms, which have developed along several different lines. These appear to represent early offshoots from the primitive stem of the Geometroidea; offshoots which have suffered much extinction or never developed to any large extent. In Australia, owing to less competition from the other families, some of these offshoots have developed to a moderate extent. Elsewhere the surviving genera and species are few. From this generalized family the other families have developed. It will be interesting to follow this development in the radial veins of the forewing. We commence with *Xenogenes* (Fig. 53a) of the Oenochromidae with its primitive areole and R1 arising separately. In *Epidesmia* R1 anastomoses with the areole, forming what has been conveniently named a double areole. Strictly speaking, however, the posterior of the twin cells is the areole, the anterior is a new formation, which we may call a pseudoareole. In the Larentiadae the areole persists; the pseudoareole also often persists as in *Cidaria*, but frequently it is lost by coalescence, thus restoring the single areole; in a few genera of this family the single areole has also been lost by coalescence. In *Acodia pauper* a curious condition occurs, in which the areole has disappeared in most, but not all, specimens by failure of its posterior wall (represented in the figure by a dotted line) to chitinize. The same abnormal neuration is developed as a rare aberration in other species, in which the areole is normally intact (see Figs. 53, a-h).

The family Sterrhidae has developed along a different line. Here both areole and pseudoareole are present in *Autanepsia* and *Organopoda*. More frequently only a single cell, which is the pseudoareole, is developed, and the radial veins arise on a common stalk from well before the end of the cell as in *Brachycola*. The same transformation has occurred in the larentiad genus *Cataclysmes*. It can hardly be doubted that this form of neuration is also the result of a failure of the posterior wall of the areole to chitinize. In a few genera this pseudoareole is very small and sometimes lost by coalescence.

In one section of the Oenochromidae the areole is very long and narrow, and its very short posterior wall may either persist or disappear (by failure to chitinize) in the same species. In the family Boarmiadae, which has an areole in its earlier genera, it has disappeared in most. This disappearance of the areole by dissociation is actually the same process as recorded in the last paragraph, but is less striking, because of the smallness of the apparent change, and because the close approximation of the veins separated indicates that the loss of the connecting bar is of no mechanical importance. In the figure of a species of *Cleora* (Fig. 54) the resemblance of the neuration to that of an *Oenochroma* (Fig. 53h), in which the areole has been lost, is obvious. This is not so obvious in the figure of a species of *Boarmia* (Fig. 55), but in that and many other genera it has been obscured by great variability even in the same species. R1 may be stalked or coincident with R2, their common stalk, or R1 may be connected or anastomose with the subcostal, R2 may anastomose with R3, and other variations are possible.

In the Geometridae the areole is never developed. The neuration of their earlier genera, except for the presence of M2 in the hindwing, closely resembles that so often found in the Boarmiadae. We may say that the family Geometridae seems to begin where the Boarmiadae leaves off. Probably, however, the former arose separately from that section of the Oenochromidae, in which R1 anastomoses first with the subcostal and then with R2. Compare the forewing neurations of *Eumelea* (Fig. 57) and *Crypsiphona* (Fig. 56).

Meyrick included the Bombycoidea with the Geometroidea in a single superfamily under the name Notodontina. Certainly if the neuration were our only guide, the family Notodontidae comes very near the Oenochromidae; the only constant difference being the humeral angle all-present at the base of the subcostal of the hindwing in the Geometroidea. To this there is no exception, now that *Diceratucho* (Fig. 59) formerly referred to the Oenochromidae, has been found to be one of the Notodontidae. This difference alone would not justify the separation of the superfamilies, but Prout (1910) has pointed out a more important anatomical difference. It relates to the morphology

of the basal cavity and tympanum in the second abdominal segment and its relation to the first segment with its spiracle. (For further details regarding the Oenochromidae see Turner, 1929.)

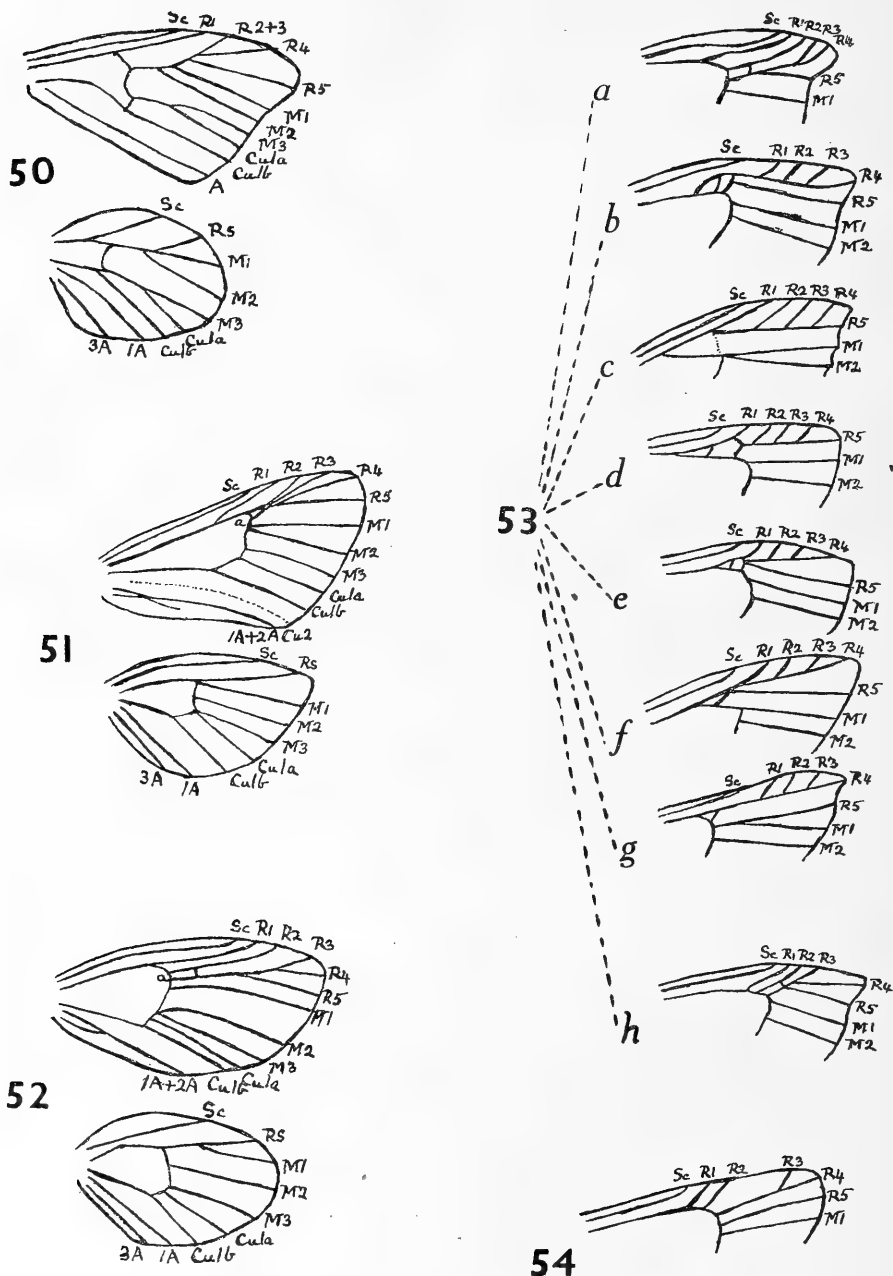


Fig. 50.—*Panacela nyctopa* Turn. Fig. 51.—*Cerura vinula* Lin. (after Meyrick). Fig. 52.—*Ochrogaster contraria* Wlk. Fig. 53.—Apical part of forewing in eight genera of Geometroidea showing variations in the structure of the areole. a. *Xenogenes eustrotiodes* Prout. b. *Epidesmia hypenaria* Gn. c. *Acodia pauper* Rosen. d. *Autanepsia poliodesma* Turn. e. *Organopoda olivescens* Warr. f. *Brachycola porphyropis* Meyr. g. *Cataclysta virgata* Roff. (after Meyrick). h. *Oenochroma vinaria* Gn. Fig. 54.—*Cleora illustraria* Wlk.

## SUPERFAMILY URANOIDEA.

Tongue present. Thorax and abdomen slender. No median vein present in cell of either wing. Forewing without areole; R1 separate or arising separately and often running into the subcostal; R3 and R4 stalked, R2 stalked with them or separate, rarely absent, R5 widely separate from R4, connate or more often stalked with M1, and M2 from middle or from above middle of cell. Hindwing with R1 absent, subcostal separate, M2 from middle or from above middle of cell; and Cu2 absent in both wings (Figs. 60-62).

This superfamily, which is of no great extent, consists of two distinct families. Its most striking character is the wide separation of R5 from R4, R5 being connate or stalked with M1.

The Uraniidae is a small and specialized group comprising some large day-flying species, though the majority are of more moderate size. In them the frenulum is absent; in the forewing 1A and 2A form a basal fork; in the hindwing 3A is absent.

Members of the family Epiplemidæ are of small size and inconspicuous coloration. They have retained the frenulum; there is no basal anal fork; in the hindwing 3A is present (Figs. 61, 62).

## SUPERFAMILY SPHINGOIDEA.

This group consists of a single isolated wide-ranging family. The species are of large or at least of moderate size. The thorax and abdomen are robust. The tongue is usually well developed and sometimes extremely long, but in a few genera, short and weak. The palpi are peculiar, being usually large, broad, closely applied to the head, and with a small or minute terminal joint often hidden by scales. The antennae are usually rather short or at most of moderate length, subcylindrical, often thickened towards apex, but seldom clubbed, and they have frequently an apical hook. In the wings the areole is never present and there are no median veins in the cell of either wing. In the forewing R1 arises from the cell beyond the middle, R2 is stalked or coincident with R3, R4 and R5 are stalked, M1 arises from near the upper angle of the cell, or is stalked with R4 and R5, M2 is always nearer M3 than M1, usually it arises from below the middle of the cell, but is never closely approximated to M3, Cu2 is absent and 1A and 2A are basally forked (Figs. 63, 64). In the hindwing R1 is always present, Rs is always approximated to the subcostal beyond the cell, M2 arises from the middle of the cell or from slightly above or below, Cu2 is absent, but 3A is present.

The neuration in the Sphingidae varies very little, and is consequently of little value in the internal classification of the family. Rothschild and Jordan have studied with much thoroughness (1903) other anatomical features, which they have employed for this purpose. The approximately median origin of M2 of the forewing is a generalized character, being intermediate in its position to that in the preceding and following superfamilies.

## SUPERFAMILY NOCTUOIDEA.

The maxillary palpi are rudimentary or absent (except in *Hyblaea*). There is no median vein in the cell of either wing and Cu2 is absent in both wings. The frenulum is present (only in the male in the Anthelidae). In the forewing M2 is approximated or connate with M3 at its origin. In the hindwing the subcostal usually anastomoses with the cell, and 3A is present (but often absent in the Syntomidae).

This is by far the largest superfamily in the Sthenochorda. It is a natural group of six families. These show a wide range of structural variation. The family Syntomidae is a specialized development of the Arctiidae, and lacks some of the more primitive characters that are present in some or all of the genera of the other five families. The areole is never present. The hindwing is always small and has undergone more or less reduction in the number of its veins (Figs. 65, 66). The subcostal is always completely fused with the cell and radial sector throughout, and may therefore be said to be absent. In many genera one or two other veins have been lost, the missing veins not being the same in all of them; 3A is also often absent.

The family Arctiidae has preserved the areole in its more primitive genera. When absent it has disappeared by coalescence, except in a small group of genera in which it

has disappeared by dissociation (Fig. 19). In the hindwing the subcostal has completely fused with the base of the cell and this fusion extends usually to the middle of the cell or even beyond, and in a few cases includes the base of the radial sector; M2 is approximated, connate, stalked, or coincident with M3 (Fig. 67). The retinaculum is nearly always bar-shaped; and the palpi are short. There is great variety in the neurination owing to the frequent stalking or coincidence of veins in either or both wings.

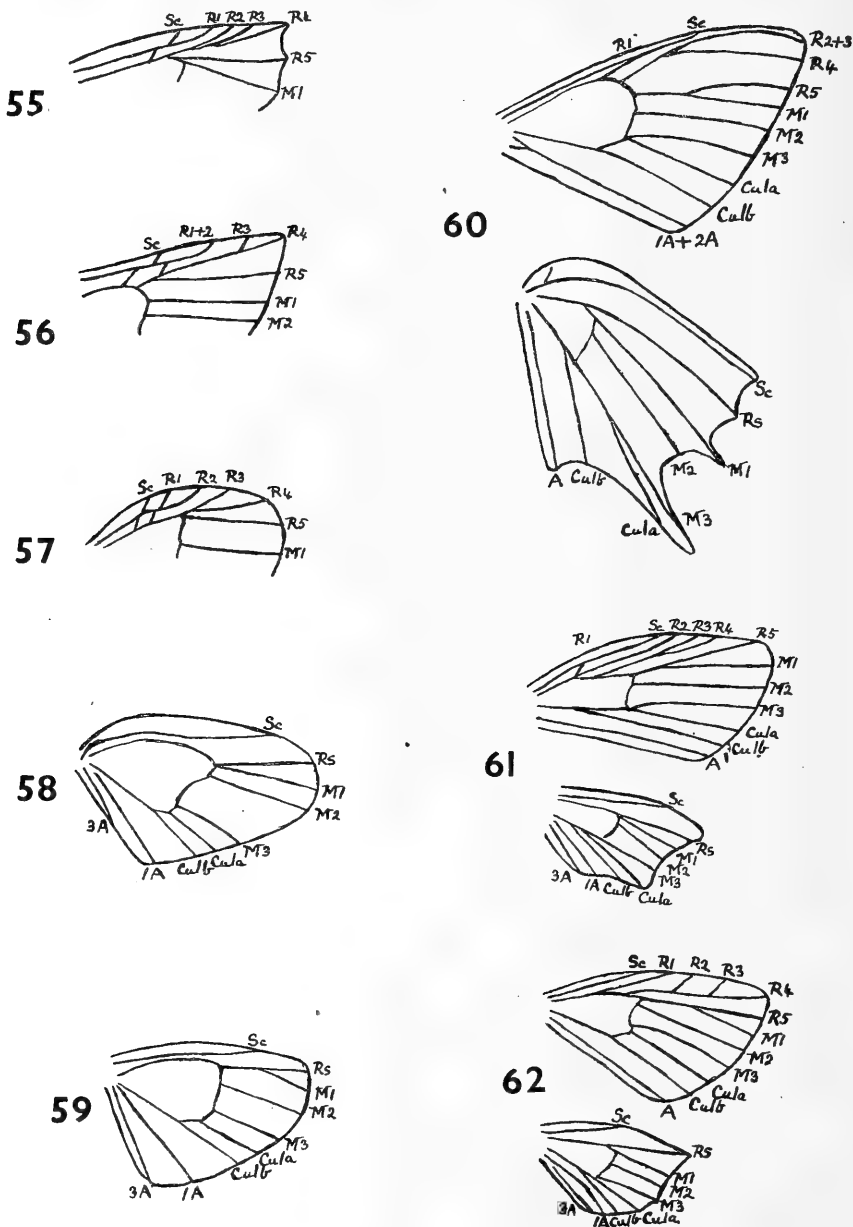


Fig. 55.—*Boarmia lyciaria* Gn. Fig. 56.—*Crypsiphona occularia* Don. Fig. 57.—*Eumelia rosalia* Stoll. Fig. 58.—*Monoctenia falernaria* Gn. Fig. 59.—*Diceratucha xenopis* Low. Fig. 60.—*Nyctalemon patroclus* Lin. Fig. 61.—*Lobogethes interrupta* Warr. Fig. 62.—*Epiplema instabilata* Wlk.



Two subfamilies may be recognized, the Arctiinae and Lithosiinae, the former with the thorax and abdomen stout and usually hairy, the latter with these slender and usually smooth. These are differences of apparently little morphological value, but they represent two distinct lines of evolution, and the division is a natural one.

The Noctuidae is an immensely numerous family, but one which presents comparatively small structural variations, the neuration being almost uniform in the great majority of its genera. In the forewing R1 arises from the cell and does not anastomose; the areole is present in probably nine-tenths of the genera, and R2 generally arises from it separately, but the areole may be lost either by coalescence or dissociation. In the hindwing the subcostal and radius arise separately from the base of the wing, but anastomose very soon, usually at a point only, but in some cases the anastomosis is prolonged as far as the middle of the cell (Figs. 68-70).

The internal classification of the family is difficult. It is divisible into two groups, Trifidae and Quadrifidae (Caradrinidae and Plusiidae of Meyrick), but these are not sharply defined. In the former, M2 of the hindwing has retained its median position, but has become vestigial. In the latter, M2 has been displaced towards, or as far as, the lower angle of the cell and remains fairly or strongly developed. There are, however, intermediate genera. The classification by Hampson into eleven subfamilies is convenient and for the most part natural, but they are not sharply defined and, therefore, incapable of strict definition. The Agaristidae have been considered a distinct family, but without justification. They are merely day-flying noctuids, and are not separated by any sharp

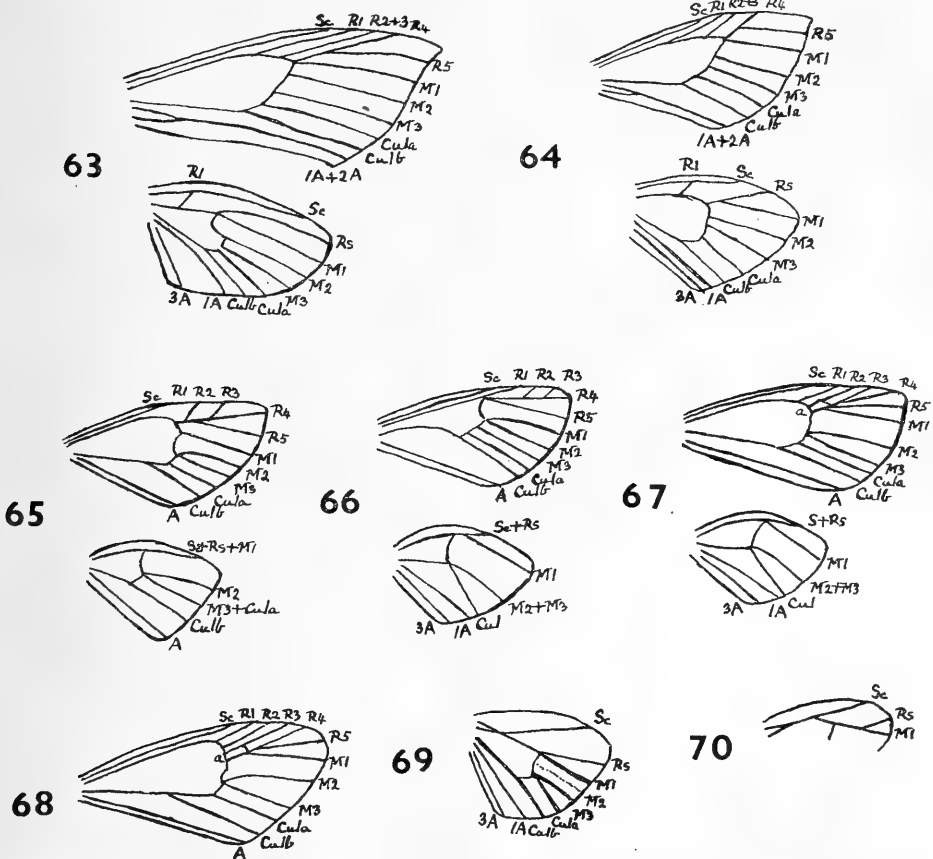


Fig. 63.—*Herse convolvuli* Lin. Fig. 64.—*Hopliocnema brachycera* Low. Fig. 65.—*Syntomis annulata* Fab. Fig. 66.—*Euchromia creusa* Lin. Fig. 67.—*Utetheisa pulchella* Lin. Fig. 68.—*Mocis frugalis* Fab. Fig. 69.—*Cosmodes elegans* Don. Fig. 70.—*Earias parallela* Luc.

line from the rest of the family. The Noctuidae cannot have been derived from any existing family, but probably arose from low down on the hypsid stem. The most primitive subfamily is perhaps the Hyblaeinae, which has well-developed maxillary palpi (alone in the Noctuoidea), but has lost the areole. The apparently rather close affinity of the Noctuidae with the Arctiadae is probably partly due to convergence.

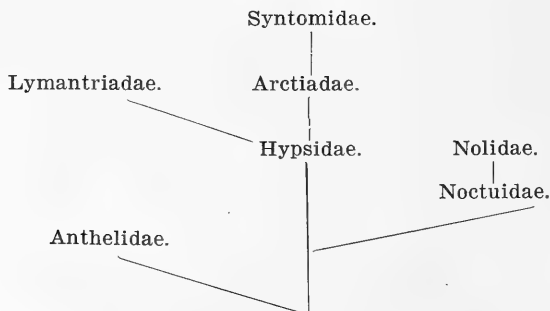
Convergence is still more noticeable in the Nolidae, a small family which cannot be distinguished from the Arctiadae by neurulation. There is no areole in the forewing; in the hindwing the subcostal and radius are completely fused from the base to about the middle of the cell; in other respects there is not much variation in the neurulation. A minor but constant characteristic is the presence of tufts of raised scales on the forewings. They appear to be directly derived from the Noctuidae, perhaps from the Sarrhothripinae.

Another small family is the Hypsidae, which is important as the direct ancestor of the Arctiadae. It differs from that family in the subcostal of the hindwing being separate from the radius from the base, but connected with it at about one-fourth by R1 or by an anastomosis (Fig. 71).

The Lymantriadae is a family of some size distinguished from the Hypsidae by the absence of the tongue, and following a different line of development. Many of the genera have retained the areole, but many have lost it, usually by coalescence, but in a few by dissociation. In the hindwing the subcostal is approximated to the radius and connected with it by R1 (Fig. 72).

The Anthelidae (Turner, 1921) is an Australian family of sixty or seventy species. In this family the tongue is absent in all but one genus. The frenulum is present in the male but absent in the female. In the forewing an areole is always present; in form it is rather large and elongate so as to reach nearly to the apex of the wing (Figs. 73, 74). At the base of the hindwing the subcostal is widely separated from the radius and usually remains so, but may be less widely separate opposite the middle of the cell. Normally these veins are connected by R1, but this may be weakly developed or absent. The most characteristic feature in the neurulation is a cross-bar from R2 to R3 at the distal end of the areole, a new development peculiar to this family (Fig. 73). In the two following genera this cross-bar extends from R1 to R3; *Gephyroneura* (Fig. 75), in which the proximal half of the areole has coalesced leaving a triangular distal portion fully developed; and *Munichryia* (Fig. 74), which is the only genus possessing a well-developed tongue.

The Anthelidae is a specialized group, which has retained some archaic peculiarities. It cannot have been derived from, or given rise to, any existing family, but probably is an early branch from the stem which gave rise to the Hypsidae and Lymantriadae. The following scheme illustrates my conception of the relationships of the families of the Noctuoidea.



SUPERFAMILY DREPANOIDEA.

There is no median vein in the cell and Cu2 is absent in both wings. Forewings with M2 from lower angle of cell. Hindwings with subcostal closely approximated to Rs near its origin, 3A short or absent.

There are two families. The Callidulidae is a small family of day-flying moths represented in India (Hampson, 1892). In them the antennae are simple and the palpi long and slender. The frenulum is sometimes short or absent. In the hindwings the cell is open; 3A is present, M2 and M3 are stalked, Rs and M1 are stalked, the subcostal is bent so as nearly to touch Rs near this point; and there may be a minute precostal spur (Fig. 78). The areole, though generally lost, is present in one genus.

The Drepanidae is a family of no great size, which presents considerable structural variation. The palpi are slender and often minute. Tongue, frenulum and areole may be present or absent. In the hindwing Rs arises well before angle of cell approximated to or (in *Amphitorna*, Fig. 81) anastomosing with the subcostal, the cell is closed and 3A may be absent; when present, it is short and usually runs to dorsum. In *Oreta* (Fig. 80) the areole is very long, reaching nearly to apex of forewing, and extremely narrow.

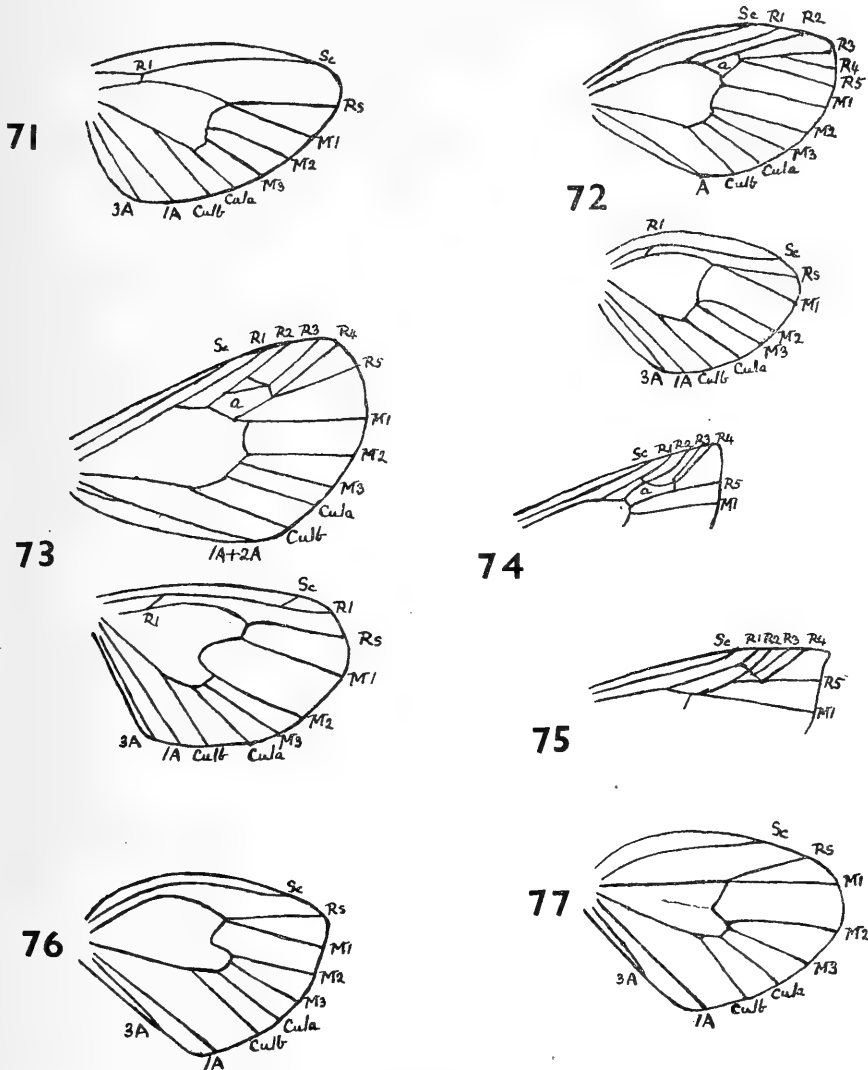


Fig. 71.—*Hypsa alciphron* Cram. Fig. 72.—*Laelia obsoleta* Fab. Fig. 73.—*Anthela ferruginosa* Wlk. Fig. 74.—*Munichryta senicula* Wlk. Fig. 75.—*Gephyroneura cosmia* Turn. Fig. 76.—*Pterolocera amplicornis* Wlk. Fig. 77.—*Nataxa flavifascia* Wlk.

This superfamily is of comparatively small extent and more nearly allied to the Noctuoidea than to any other, but should not be included with this superfamily. The neurational resemblances to the Pyraloidea are an example of convergence, the two groups being genetically widely separate. The suggestion that the Callidulidae is in any way nearly related to the Rhopalocera is in my opinion equally unfounded.

#### SUPERFAMILY LASIOCAMPOIDEA.

Of these I recognize only one family, the Lasiocampidae, which is found in all continental areas. The family is sharply distinguished from the Bombycoidea by the approximation of the origins of M2 and M3, though it has specialized, like some families of that group, by the loss of the frenulum. The areole has been lost by coalescence, not by dissociation, as I at one time supposed (1918), for that would have left R2 stalked with R3 and R4 with R5, but, on the contrary, while R2 and R3 are stalked as in other Sthenochorda, R4 remains a separate vein in nearly all the genera (Figs. 82, 83). The exceptions are the Indian genus *Bhima* and the European genus *Endromis* (Fig. 84), in which as a secondary change R4 has become stalked with R2 and R3, and the Australian *Aprosepta* Turn., in which it is stalked with R5. The basal expansion of the costal base of the hindwing, which compensates for the absence of the frenulum, is often large and usually contains one or more, and occasionally many, basal costal pseudoneuria, evidently for the purpose of strengthening this part of the wing. These are very irregular in form as well as in number, being frequently branched, and cannot therefore be due to the persistence of the humeral veinlet present in the Homoneura (Figs. 85, 86). On the contrary, the presence of these substitutes indicates that this veinlet has been irrevocably lost. In most of the genera there is a strong anastomosis enclosing a basal accessory cell between the subcostal and radial sector of the hindwing. As in other groups, this anastomosis has replaced the vein R1, which is still present in a few genera. The most primitive in this respect is *Endromis* (Fig. 84), in which a short R1 is present as occurs in many other families. For the strengthening of this part of the wing two lines of evolution have developed: (1) a strong anastomosis with a moderate accessory cell in most genera, or (2) a grossly exaggerated accessory cell with retention of R1 as in *Perna* (Fig. 83).

I see no sufficient justification for retaining the Endromidae as a separate family containing the single genus *Endromis*.

#### SUPERFAMILY PSYCHIOIDEA.

Tongue absent. Frenulum developed. In both wings a median vein, which may be either single or forked, is present in the cell. In the forewings M1 arises from the middle of the cell or slightly above, M2 is approximated to, or connate with, M3, and R3 and R4 are stalked or rarely coincident. In the hindwings M2 is connate, stalked, or coincident with M3. Cu2 is present in both wings.

In this and the two following superfamilies the median vein persists in the cell, but chorda and areole are never present in the Psychoidea. It consists of two families, one specialized, the other more generalized, both probably ancient offshoots of a common stock.

In the Psychidae the female never leaves the larval case, and has usually degenerated into little more than an egg-sac, though antennae and legs are present in the most primitive genera. In both sexes the tongue and palpi are absent. The neuration of the male is in most cases highly peculiar, but this is not so in the most primitive genera. Of these *Aprata* (Fig. 87) from Ceylon is a good example. Here the neuration is of a generalized character. The European genus *Fumea* (Fig. 88) differs in the loss of the lower branch of the median in the cell of both wings, the coincidence of R3 and R4 of the forewings, and the loss of one of the branches of the median beyond the cell in the hindwings. In the great majority of genera the forking of the median is preserved in the cell of both wings. Their neuration in some respects shows features unique in the Lepidoptera. In most, the combined first and second anals of the forewing run upwards to fuse with the second cubital. The second anal may be continued beyond its anastomosis even to the wing margin, and sometimes several veinlets or pseudo-

neuria arise running from the combined anal vein towards the dorsal margin. In *Clania ignobilis* (Fig. 90) the combined R1 and subcostal anastomose with Rs near the wing margin, a remarkable character. These developments appear to have arisen to strengthen the areas of wing affected. They are probably adaptational and therefore only of minor genetic significance. Accessory veinlets, variable in number, may develop, running towards the dorsum of the forewing and the costa of the hindwing.

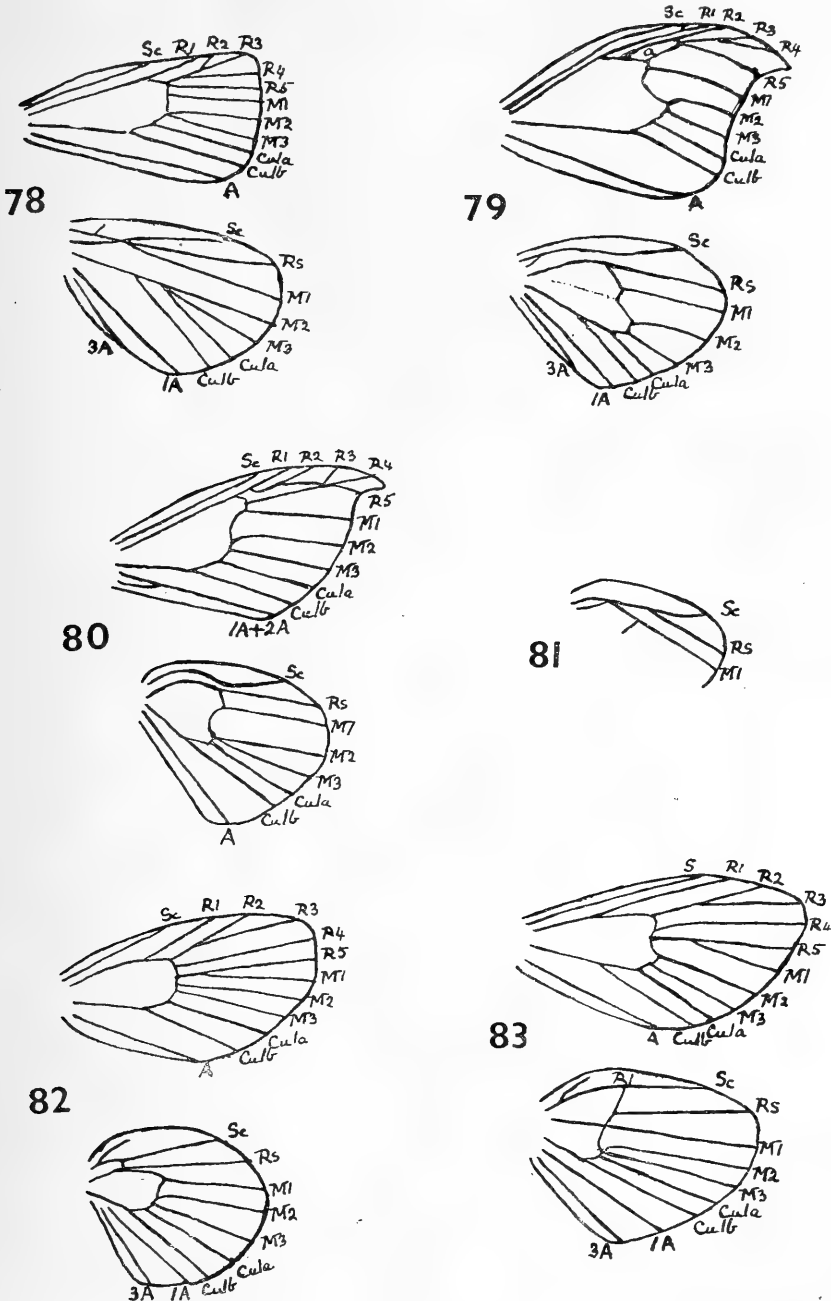


Fig. 78.—*Callidula erycinoides* Wlk. (after Hampson). Fig. 79.—*Falcaria falcataria* Lin. (after Meyrick). Fig. 80.—*Oreta jaspidea* Warr. Fig. 81.—*Amphitorna lechriodes* Turn. Fig. 82.—*Eriogaster rubi* Lin. (after Meyrick). Fig. 83.—*Perna exposita* Lewin.

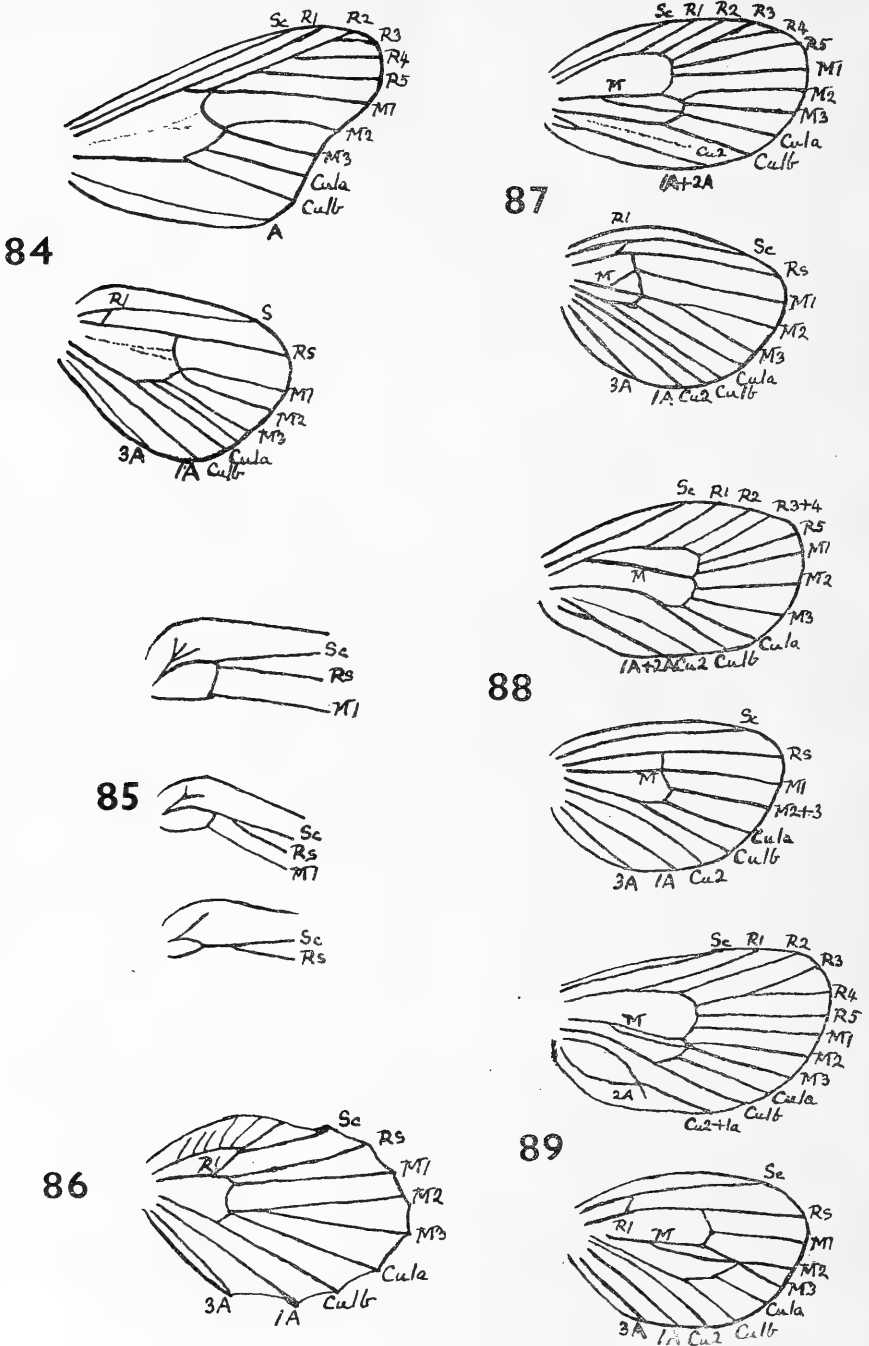


Fig. 84.—*Endromis versicolora* Lin. (after Meyrick). Fig. 85.—Humeral angle of hindwing in three genera of Lasiocampidae. a. *Porola arida* Wlk. b. *Crexa subnotata* Wlk. c. *Bombycomorpha pallida* Dist. Fig. 86.—*Gastropacha quercifolia* Lin. (after Meyrick). Fig. 87.—*Aprata mackwoodi* Moore (after Hampson). Fig. 88.—*Fumea casta* Pall. (after Meyrick). Fig. 89.—*Plutorectis lurida* Heyl.

In the Limacodidae the median vein in the cell of the forewings is usually, but not always, single; in the hindwings it is always unbranched. There is not much variation in the neuration, the most important being in R1 of the hindwings, which is present in the older genera, but in many is replaced by an anastomosis (Figs. 91, 92). Although the frenulum is well developed, the base of the hindwings may be rather strongly curved and in some cases fine pseudoneuria from the subcostal have developed, analogous to those in the Lasiocampidae.

#### SUPERFAMILY CASTNIOIDEA.

In this group the labial palpi are well developed. The tongue may be present or absent. The antennae are smooth and dilated or clubbed at their apices. A forked or single median vein is present in both wings. In the forewing Cu2 is present and M2 is approximated at its origin to M3.

Of the two families of which it is composed the Castniidae is the more primitive. In this family the cell is closed in both wings; Cu2 and two anal veins are present in the hindwings; and there is a well-developed areole in the forewings (Figs. 94, 95). The family is exclusively neotropical.

The family Tascinidae has lost the areole, and the cell is open in the hindwings, and sometimes in the forewings also. The hindwings have two anal veins, but Cu2 is absent. The family is represented in Australia by the genus *Synemon* (Fig. 93) and in Malaya by two closely allied genera, *Tascina* (Fig. 96) and *Neocastnia*. In the latter two the hindwing neuration shows complete absence of the discocellulars so that the median vein and its lower branch (the upper branch being obsolete), with its sub-branches M2 and M3, are isolated. The cell of the forewings is open in its costal half. In *Synemon* the cell is closed in the forewings; in the hindwings the discocellular between M1 and M2 is absent, but the connection between M3 and Cu1a is retained.

Members of the superfamily Castnioidea are day-flying moths often on the wing in bright sunshine, and with this appears to be correlated their clubbed antennae and superficial form, which have suggested some affinity with the Hesperidae and other Rhopalocera. An examination of the neuration is sufficient to dispel this supposition. In reality there are hardly two groups of the Lepidoptera more distinct. The superfamily is isolated, and probably an ancient development from the same stem as the Cossioidea, which are their nearest allies. This is strongly confirmed by the little we know of their larvae. That of a species of *Castnia* is an internal feeder in the stem of one of the Bromeliaceae (Westwood, 1877); that of a *Synemon* forms tunnels among the roots of grasses and sedges (Tindale, 1928). Both pupate in cocoons, those of the latter being underground.

#### SUPERFAMILY COSSOIDEA.

Tongue absent. Labial palpi moderate, short, or absent. Frenulum usually present. Forewings with areole usually well developed, but sometimes small or absent, a strong median vein in cell usually forked, M2 from nearer M3 than M1, Cu2 usually present, and A1 coalescing with A2 near base. Hindwings with median vein in cell usually forked, R1 joining Sc at or near end of cell, but sometimes absent, Cu2 present, two or three anal veins, A1 and A2 coalescing near base or wholly fused. The larvae are wood-borers.

The genera *Cossodes* and *Dudgeona*, with their primitive neuration and well-developed palpi and tibial spurs, are not far from the point at which the Sthenochorda and the Asthenochorda diverged by the loss of the primitive five-jointed maxillary palpi in the former.

I have dealt fully elsewhere with the Cossidae (1918), so that it is necessary to deal here only with two small allied groups. Two genera from Madagascar have lost Cu2 in both wings, and have been separated by Hampson as the Argyrotypidae. In other respects they agree with the Cossidae, and should, I think, be included in that family. The Arbelidae are represented by some thirty or more species in Africa and India. They have lost the frenulum. The median is unbranched in both wings, there is no areole, and Cu2 is absent in both wings. The larvae are wood-borers.

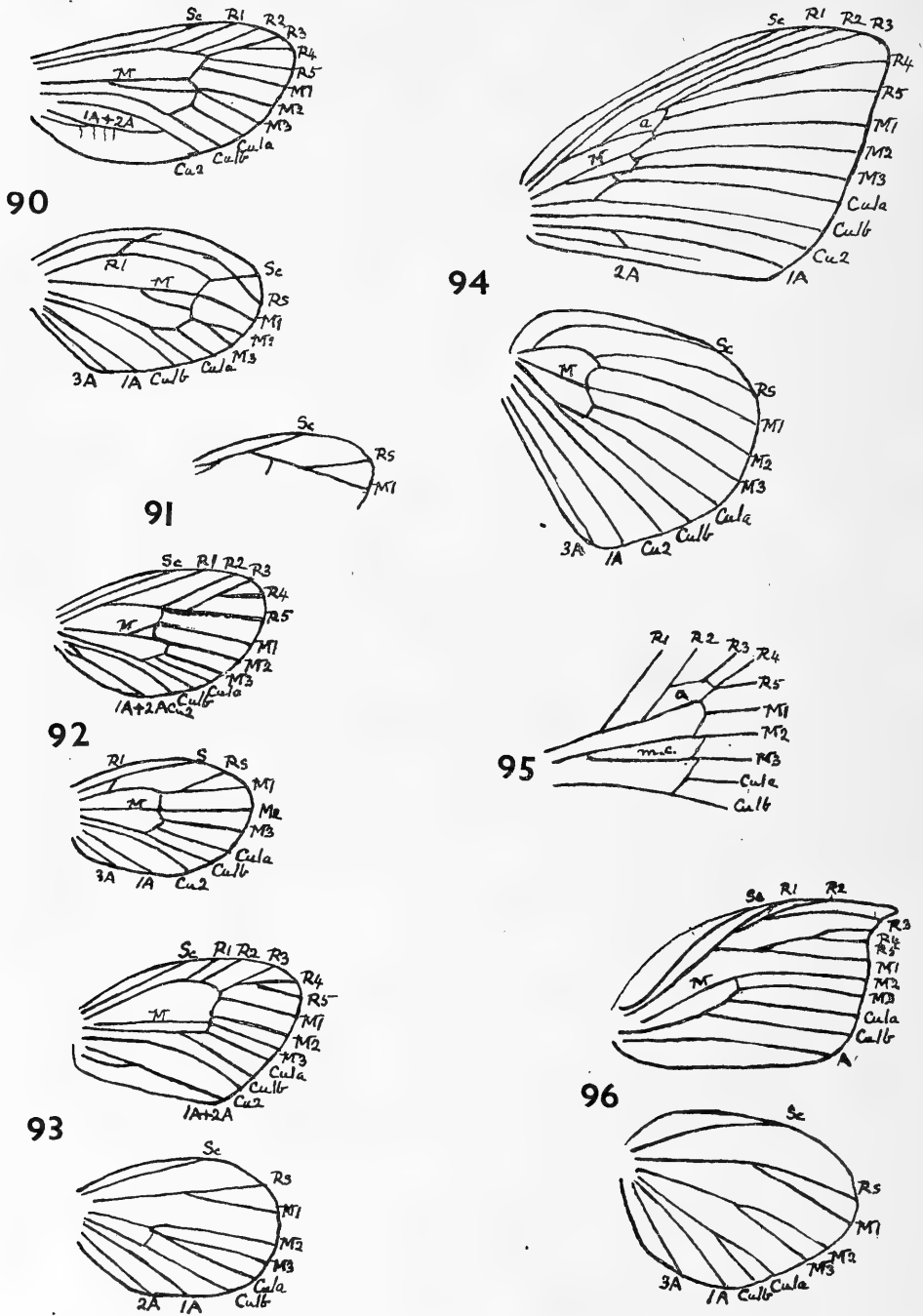


Fig. 90.—*Clania ignobilis* Wlk. Fig. 91.—*Doratifera vulnerans* Lewin. Fig. 92.—*Susica humeralis* Wlk. Fig. 93.—*Synemon collecta* Swin. Fig. 94.—*Castnia cacica* H-Sch. (after Westwood). Fig. 95.—*Gazera linus* Fab. Forewing. Fig. 96.—*Tascina orientalis* West.



## CONCLUSION.

This concludes my review of the classification of the Lepidoptera. It has, I know, some weak points, but I am confident that it represents an advance in the classification of this Order of insects. Few, perhaps, will accept its conclusions on a first reading, but it will deserve attention by anyone who attempts a future classification. I cannot conclude without expressing the debt I owe to Dr. R. J. Tillyard, whose brilliant researches inspired me to make this attempt, which I have long meditated. I grieve that he is no longer among us to read it and send me his criticisms.

## A SUMMARY OF THE CLASSIFICATION PROPOSED.

This does not contain all the families of the Lepidoptera, for I have thought it wiser to omit some, of which I have insufficient knowledge, but contains those known to occur in Europe, Australia and New Zealand, with a few that are known only from other regions.

## Suborder HOMONEURA.

Superfam. Micropterygoidea.

Fam. Micropterygidae.

Eriocranidae.

Mnaesarchaeidae.

Superfam. Hepialidoidea.

Fam. Prototheoridae.

Anomoseidae.

Palaeosetidae.

Hepialidae.

## Suborder HETERONEURA.

Division ASTHENOCHORDA.

Subdivision *Rhopalocera*.

Superfam. Hesperoidea.

Fam. Hesperidae.

Superfam. Papilionoidea.

Fam. Papilionidae.

Superfam. Nymphaloidea.

Fam. Nymphalidae.

Pieridae.

Lycaenidae.

Subdivision *Microptila*.

Fam. Elachistidae.

Subfam. Coleophorinae.

Scythrinae.

Elachistinae.

Douglasianae.

Cosmopteryginae.

Fam. Gelechiidae.

Subfam. Hyponomeutinae.

Amphitherinae.

Thalmarcellinae.

Oecophorinae.

Blastobasinae.

Gelechianae.

Xyloryctinae.

Fam. Tortricidae.

Subfam. Chlidanotinae.

Eucosminae.

Tortricinae.

Phalonianae.

## Suborder HETERONEURA.

Division ASTHENOCHORDA.

Subdivision *Microptila*.

(Continued.)

Fam. Copromorphidae.

Subfam. Copromorphinae.

Carposininae.

Fam. Aegeriidae.

Fam. Glyphipterygidae.

Subfam. Glyphipteryginae.

Heliodininae.

Heliozelinae.

Fam. Plutellidae.

Subfam. Plutellinae.

Epermenianae.

Gracilarianae.

Fam. Tineidae.

Subfam. Adelinae.

Lamproninae.

Tineinae.

Lyonetianae.

Oposteginae.

Cyclotorninae.

Epipyropinae.

Fam. Nepticulidae.

Superfam. Pterophoroidea.

Fam. Orneodidae.

Pterophoridae.

Superfam. Pyraloidea.

Fam. Thyrididae.

Phycitidae.

Galleriidae.

Crambidae.

Schoenobiadae.

Pyralidae.

Pyraustidae.

Tineodidae.

Superfam. Zygaenoidea.

Fam. Zygaenidae.

Division STHENOCHORDA.	Superfam. Drepanoidea.
Superfam. Cossoidea.	Fam. Callidulidae.
Fam. Arbelidae.	Drepanidae.
Cossidae.	Superfam. Sphingoidea.
Superfam. Castnioidea.	Fam. Sphingidae.
Fam. Castniidae.	Superfam. Uranoidea.
Tascinidae.	Fam. Uranidae.
Superfam. Psychoidea.	Epiplemidae.
Fam. Psychidae.	Superfam. Geometroidea.
Limacodidae.	Fam. Oenochromidae.
Superfam. Lasiocampoidea.	Boarmiadae.
Fam. Lasiocampidae.	Geometridae.
Superfam. Noctuoidea.	Sterrhidae.
Fam. Anthelidae.	Larentiadae.
Noctuidae.	Superfam. Bombycoidea.
Nolidae.	Fam. Saturniidae.
Hypsidae.	Bombycidae.
Lymantriadae.	Brahmaeidae.
Arctiidae.	Cymatophoridae.
Syntomidae.	Notodontidae.

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*R. J. Lillyard*

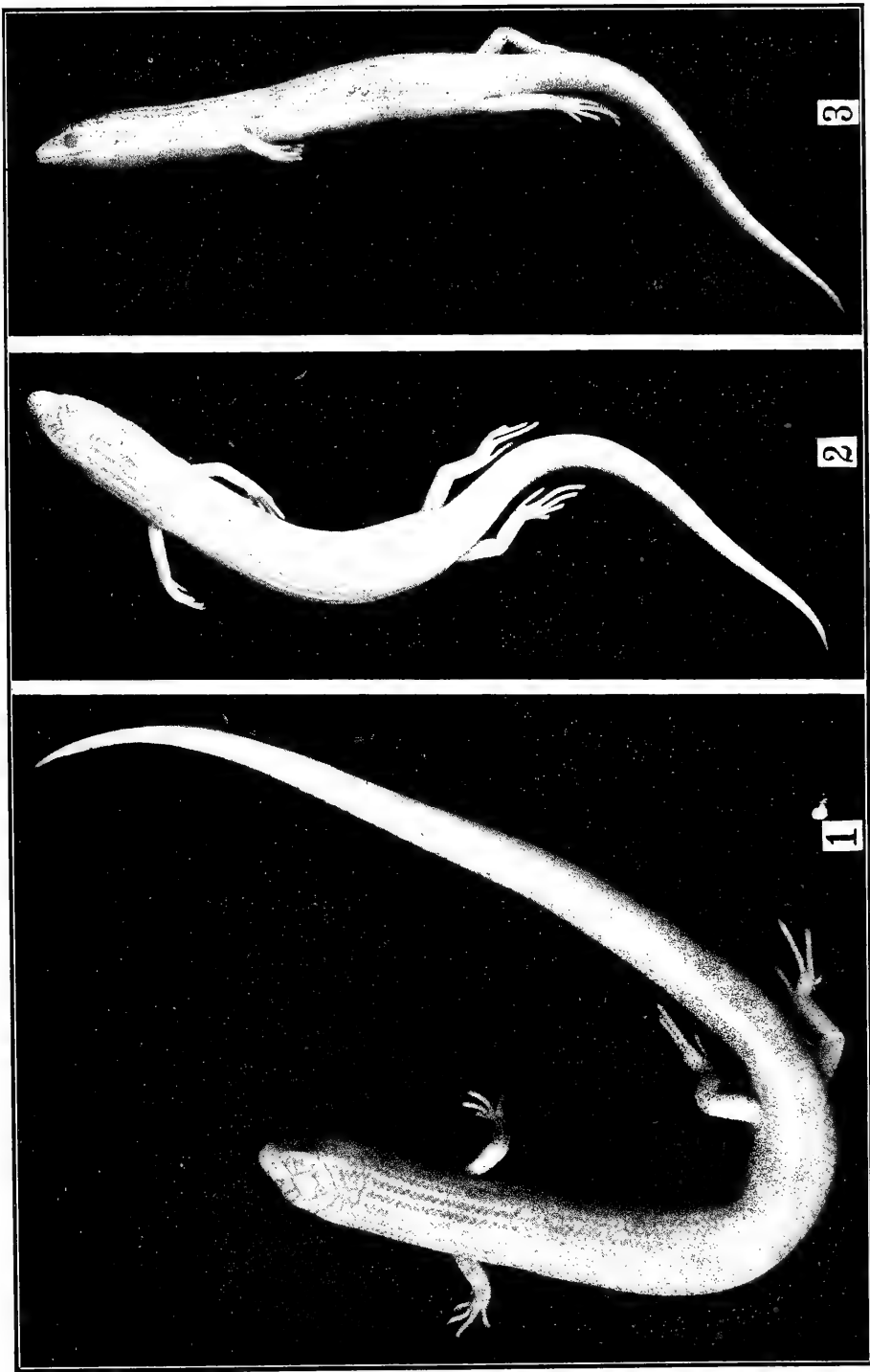
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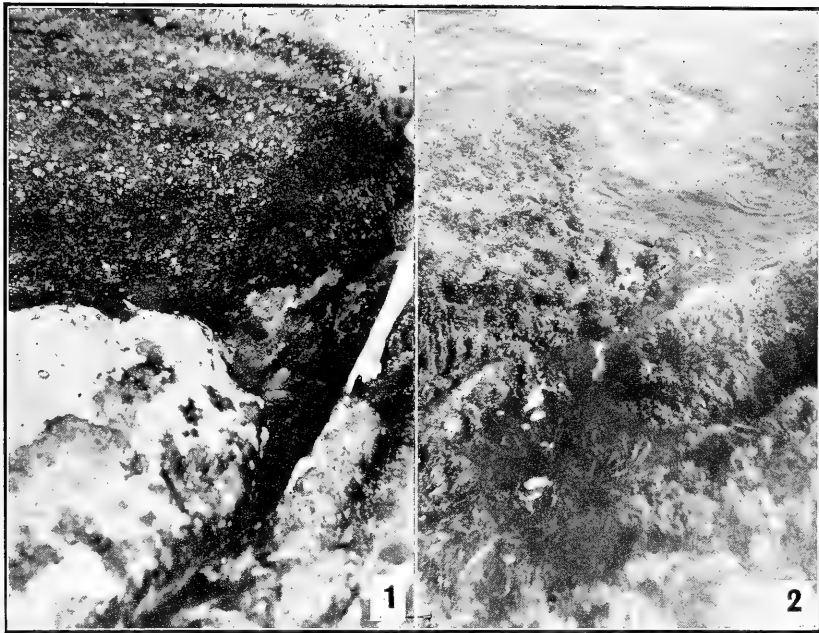
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Taxonomic Notes on the Genus *Ablepharus*.





Studies on Australian Marine Algae.





(Issued 5th November, 1946.)

Vol. LXXI.  
Parts 1-2.

Nos. 323-324.

THE  
PROCEEDINGS  
OF THE  
LINNEAN SOCIETY  
OF  
NEW SOUTH WALES

FOR THE YEAR  
1946.

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*Parts I-II (Pages i-xxi; 1-71).*

CONTAINING THE PROCEEDINGS OF THE ANNUAL MEETING  
AND PAPERS READ IN MARCH-APRIL.

With two plates.  
[Plates i-ii.]

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PRINTED AND PUBLISHED FOR THE SOCIETY BY  
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SOLD BY THE SOCIETY,  
Science House, Gloucester and Essex Streets, Sydney.

1946.  
PRICE 6/9.

Registered at the General Post Office, Sydney, for transmission  
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† Elected to Council 17th April, 1946.

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1875-76	3 0	3 0	5 0	7 6	1899	12 6	12 0	10 0	10 6
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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 <sup>3</sup>	15 0
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BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 28th FEBRUARY, 1946.

LIABILITIES.		ASSETS.	
	£ s. d.		£ s. d.
Accumulated Funds—		Fixed Assets—	
Amount bequeathed by Sir William Macleay ..	12,000 0 0	Commonwealth Loans, at cost .. .. .	16,320 0 0
Accumulated Income Capitalized .. .. .	3,820 0 0	Current Assets—	
		Commercial Banking Company of Sydney Ltd. . . . .	602 18 6
		Commonwealth Savings Bank .. .. .	312 10 10
Income Account at 28th February, 1946 .. . . .	15,820 0 0	Cash in hand .. .. .	6 0 0
	1,421 9 4		
	<u>£17,241 9 4</u>		<u>£17,241 9 4</u>

INCOME ACCOUNT. Year Ended 28th February, 1946.

	£ s. d.		£ s. d.
To Salaries .. .. .	760 8 4	By Balance from 1944-45 .. .. .	1,154 18 5
" Expenses .. .. .	16 11	" Interest .. .. .	630 0 4
" Petty Cash .. .. .	2 4 2	" Donations (Assistant to Bacteriologist) .. . . .	400 0 0
" Balance to 1946-47 .. .. .	1,421 9 4		
	<u>£2,184 18 9</u>		<u>£2,184 18 9</u>

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1946, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1946, as shown by the books. Certificates of the investments have been inspected.

Sydney, 12th March, 1946.

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

A. B. WALKOM,  
Hon. Treasurer.  
4th March, 1946.

# PROCEEDINGS, LXXI, PARTS 1-2, 1946.

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(Issued 15th January, 1947.\*)

Vol. LXXI.  
Parts 3-4.

Nos. 325-326.

THE  
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LINNEAN SOCIETY

OF  
NEW SOUTH WALES

FOR THE YEAR

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[Plates iii-xvi.]

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1892	10 0	9 6	17 0	7 6	1915	13 0	17 0	25 0	19 0
1893	6 6	4 6	8 0	8 0	1916	17 0	12 6	10 0	11 0
1894	5 0	11 0	6 0	9 0	1917	10 0	12 0	15 0	19 0
1895	12 0	12 0	13 0	8 0	1918	14 0	9 0	12 6	16 6
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AUSTRALASIAN MEDICAL PUBLISHING CO., LTD.,  
Seamer Street, Glebe, Sydney,

and

SOLD BY THE SOCIETY,  
Science House, Gloucester and Essex Streets, Sydney.

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Registered at the General Post Office, Sydney, for transmission  
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