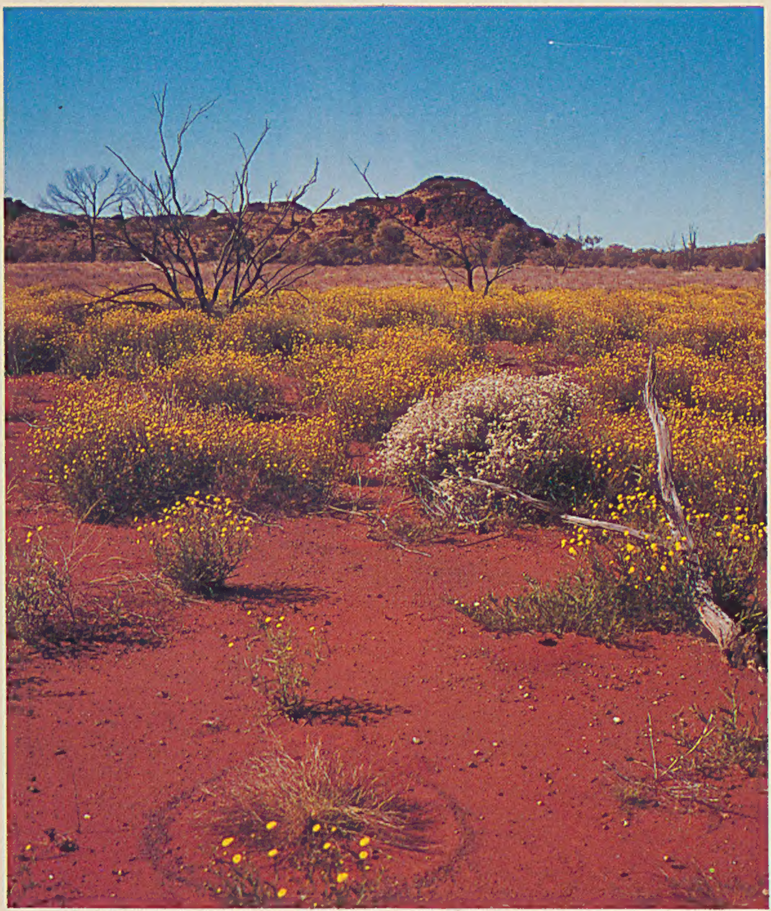
FLORA OF AUSTRALIA

Volume 1
Introduction



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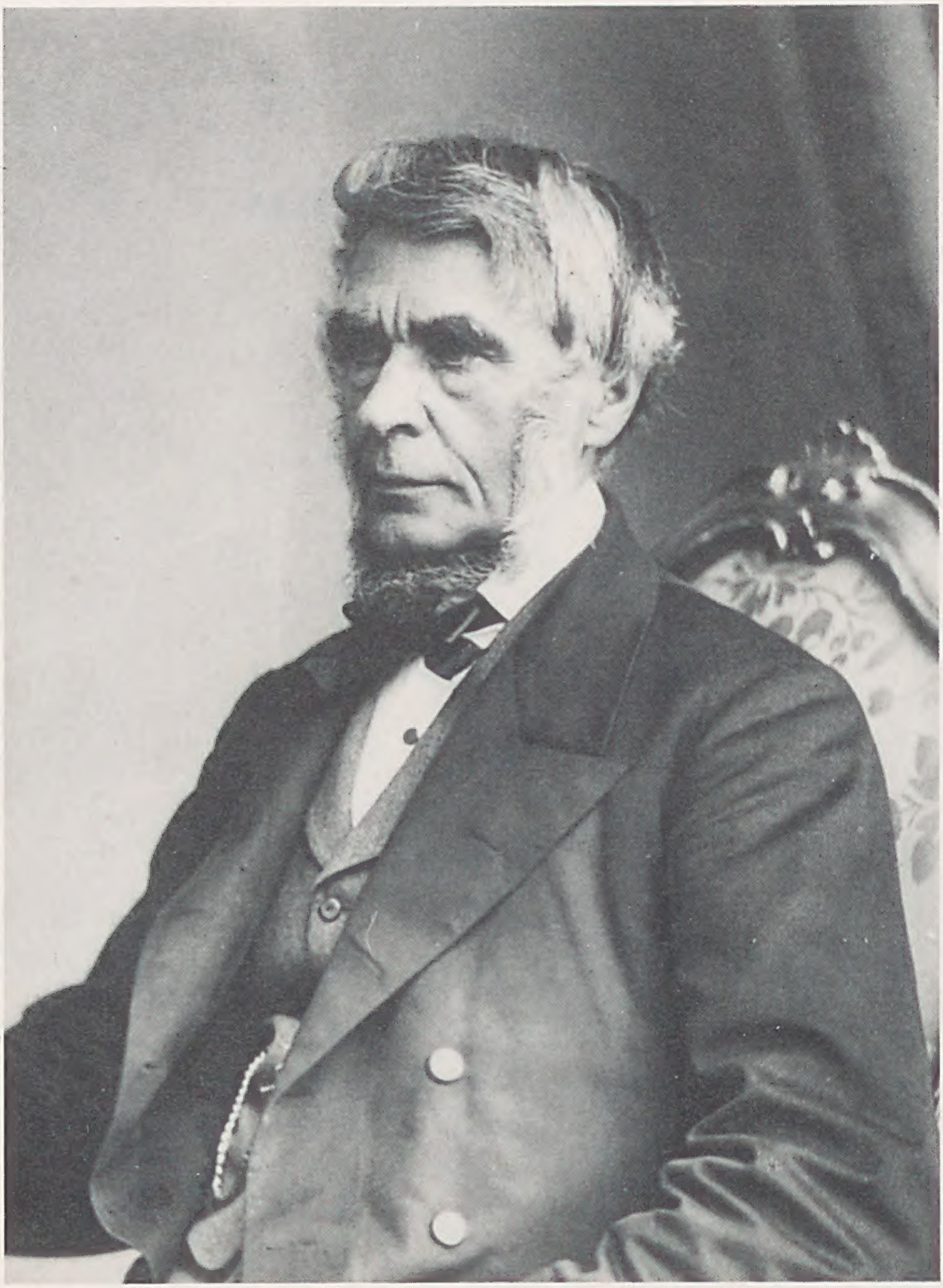
FLORA OF AUSTRALIA



George Bentham (1800–1884), author of *Flora Australiensis*, the only previous complete Australian Flora. Reproduced by courtesy of the Director, Royal Botanic Gardens, Kew.

BUREAU OF FLORA AND FAUNA, CANBERRA

FLORA OF AUSTRALIA

Volume 1
Introduction

Australian Government Publishing Service Canberra 1981

ISBN 0 642 06652 3 (case bound)
ISBN 0 642 06653 1 (soft bound)

EDITORIAL COMMITTEE

Printed at Griffin Press Limited, Marion Road, Netley, South Australia.

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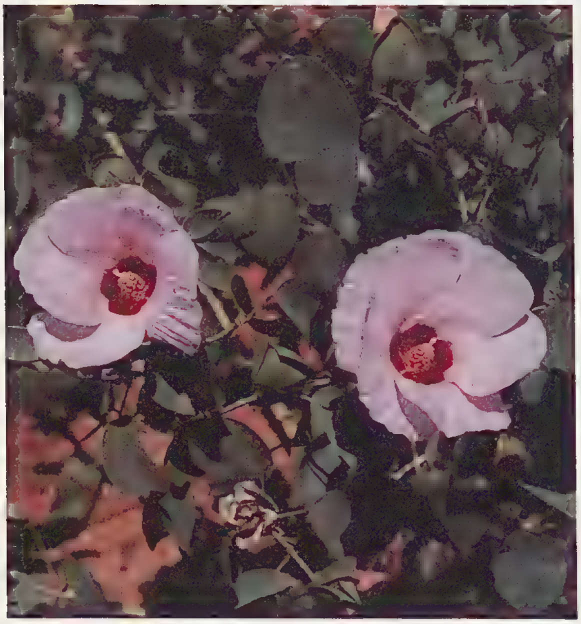
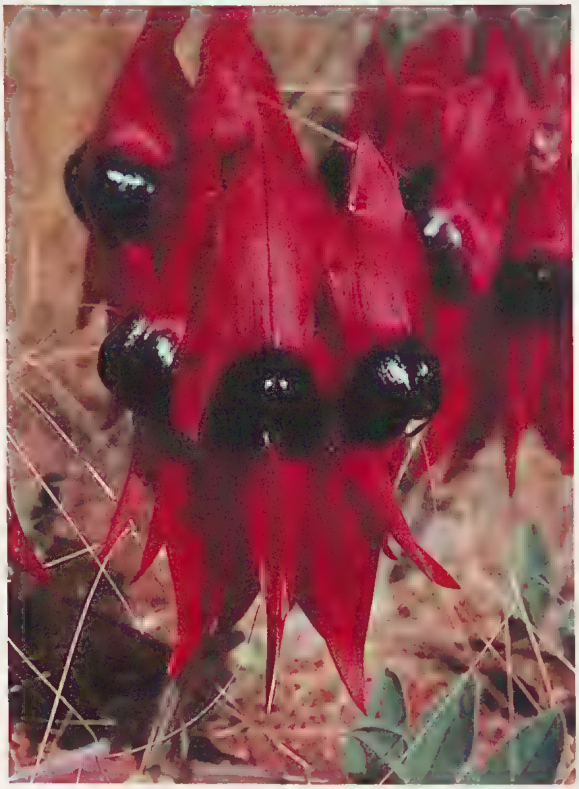
FLORAL EMBLEMS OF AUSTRALIA AND ITS STATES





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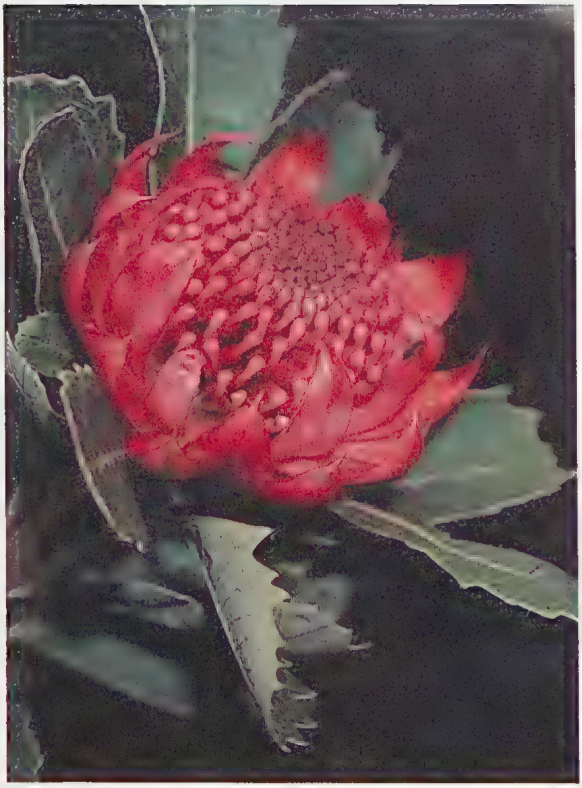

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Photograph — I. G. Holliday.


AUSTRALIA
SCALE
100 0 200 400 600 Kilometres
INDONESIA
Darwin
Derby
Cairns
Alice Springs
Brisbane
Sydney
Adelaide
Melbourne
Perth
Hobart
NORTHERN TERRITORY
WESTERN AUSTRALIA
SOUTH AUSTRALIA
QUEENSLAND
NEW SOUTH WALES
VICTORIA
A.C.T.
TASMANIA
GULF OF CARPENTARIA
CORAL SEA
PACIFIC
OCEAN
INDIAN
OCEAN
GREAT AUSTRALIAN BIGHT
SOUTHERN OCEAN
BASS STRAIT
Tropic of Capricorn
12°
18°
24°
30°
36°
110°
116°
122°
128°
134°
140°
152°

INTRODUCTION

The *Flora of Australia* is intended for use by professional botanists and other scientists, knowledgeable amateurs and students requiring botanical information. It will include all flowering and non-flowering plants known to be indigenous or naturalised in Australia but will exclude bacteria.

The geographical area covered by the *Flora* includes the six Australian States, the Northern Territory, the Australian Capital Territory, immediate offshore islands and Macquarie Island. Other Australian-administered territories, such as Lord Howe Island and Christmas Island, are excluded. The occurrence in those territories of species included in the *Flora* will be added to the notes on distribution. A complete Flora of those territories is proposed as a separate volume.

Nomenclatural coverage will comprise accepted names together with synonyms relevant to Australia, all with references to the original publication and type collections. Where necessary, new taxa and new combinations will be published in an appendix in the relevant volume. Significant references to families and genera will be cited. Author abbreviations follow the *Draft Index of Author Abbreviations compiled at the Herbarium, Royal Botanic Gardens, Kew* (HMSO, 1980). Journal titles are abbreviated in accordance with G. H. M. Lawrence et al., *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, 1968), and other literature in accordance with F. A. Stafleu and R. S. Cowan, *Taxonomic Literature*, edn 2 (W. Junk, 1976–), except that upper case initial letters are used. The abbreviation 'Austral.', for 'Australia' and its derivatives, is used consistently except that this publication, *Flora of Australia*, is cited as 'Fl. Australia' in order to avoid confusion with *Flora Australiensis* ('Fl. Austral.').

Descriptions will be concise. They will be based on Australian material except where a broader view is necessary (especially in descriptions of families or genera) to avoid giving misleading taxonomic information. Distributional data will be given in both descriptive and mapped forms. A selection of up to five representative collections will be cited for each species. All herbarium sheets examined for the *Flora of Australia* will be so labelled. Verified ecological information and chromosome numbers will be included, and phytochemical information added if of special interest.

The system of A. J. Cronquist has been adopted for the arrangement of families. The sequence for those families occurring in Australia is included on the front endpapers of this volume and will be reproduced in all subsequent volumes. The families are listed alphabetically on the back endpapers as an index to volumes. Volumes will be issued out of numerical sequence, the order to be determined largely by the availability of specialist contributors or of recent revisions on which flora treatments can be based. Within families, genera and species will be arranged so as to show natural relationships as far as possible. Because the *Flora* will be based largely on existing knowledge, the standard of treatment will vary from group to group. For the same reason it will sometimes be necessary to make arbitrary decisions on points of taxonomy and nomenclature, for example, in this volume, the spelling of *Brachycome*.

A glossary defining botanical terms is included in this volume. Specialised terms used in certain groups of plants will be explained in supplementary glossaries in the relevant volumes.

Acknowledgments

Many people have co-operated to bring the *Flora of Australia* project to fruition. Botanists throughout Australia and in other countries have contributed, either individually or through their institutions, to planning the *Flora* and to the evolution of the format. Many have commented constructively on the chapters in Volume 1, especially the Key to Families and the Glossary.

Arthur. J. Cronquist, New York Botanical Garden, made available a draft of the latest version of his system of classification for use in planning the arrangement of families. He responded promptly to requests for advice in allocating genera to families. Robert. F. Thorne, Rancho Santa Ana Botanic Garden, and Rolf. M. T. Dahlgren, Botanic Museum of the University of Copenhagen, provided the latest information on their phylogenetic systems of classification for use in the chapter by Kanis. The Director, Royal Botanic Gardens, Kew, made available copies of portraits of Bentham, Lindley, Hooker and Mueller for the frontispiece and Figures 4–6. The portrait of Brown (Figure 2) is reproduced by courtesy of the Linnean Society of New South Wales. Colin Totterdell, Division of Plant Industry, CSIRO, provided photographs for Figures 1, 3, 7, 8, and 14–17. Elizabeth Kemp, Bureau of Mineral Resources, provided copies for Figures 9–13. Sue Craven prepared the map of Australia facing page 1. Helen Hewson prepared Figures 23–26.

The Key to Families of Flowering Plants in Australia is modified from *Keys to the Families and Genera of Queensland Flowering Plants (Magnoliophyta)* by H. T. Clifford and Gwen Ludlow, edn 2 (University of Queensland Press, 1978). Those keys were based on an unpublished key prepared by the late A. Cayzer. They have been used widely in Queensland but less so elsewhere in Australia. Comments on the key will be welcomed by the Executive Editor.

Special effort was needed to produce Volume 1 in time for the XIII International Botanical Congress in Sydney, August 1981. The assistance of the Commonwealth Government, especially the Department of Home Affairs and Environment and the former Department of Science and the Environment, is acknowledged for co-operation in achieving this goal. David Ride, the first Director of the Bureau of Flora and Fauna, and later Alison McCusker as Acting Director, have carried most of the administrative responsibilities in establishing the *Flora* program. Alison McCusker also assisted in editing Volume 1. The staff of the Bureau has enthusiastically undertaken its part in preparing the volume. Arthur Chapman assisted greatly in editing and proof-reading. John Busby developed typesetting procedures and typeset this volume, using facilities of the Bureau of Flora and Fauna and the Division of Computing Research, CSIRO. Wendy Riley and Geetha Sriprakash typed the manuscript. David Marshall and Jennifer Longstaff, Australian Government Publishing Service, assisted and advised with designing the book. Jennifer Longstaff designed the cover.

Sir Rutherford Robertson has given the *Flora* project support over many years. As a Fellow and former President of the Australian Academy of Science, he played a leading role in the initiatives that resulted in the establishment of the Bureau of Flora and Fauna to co-ordinate the Australian Biological Resources Study, of which the *Flora of Australia* project forms a major part. Further, as the first Chairman of the Editorial Committee, he has firmly guided the project during its first year.

THE BACKGROUND TO THE *FLORA OF AUSTRALIA*

A. S. George

History of the *Flora of Australia* Project

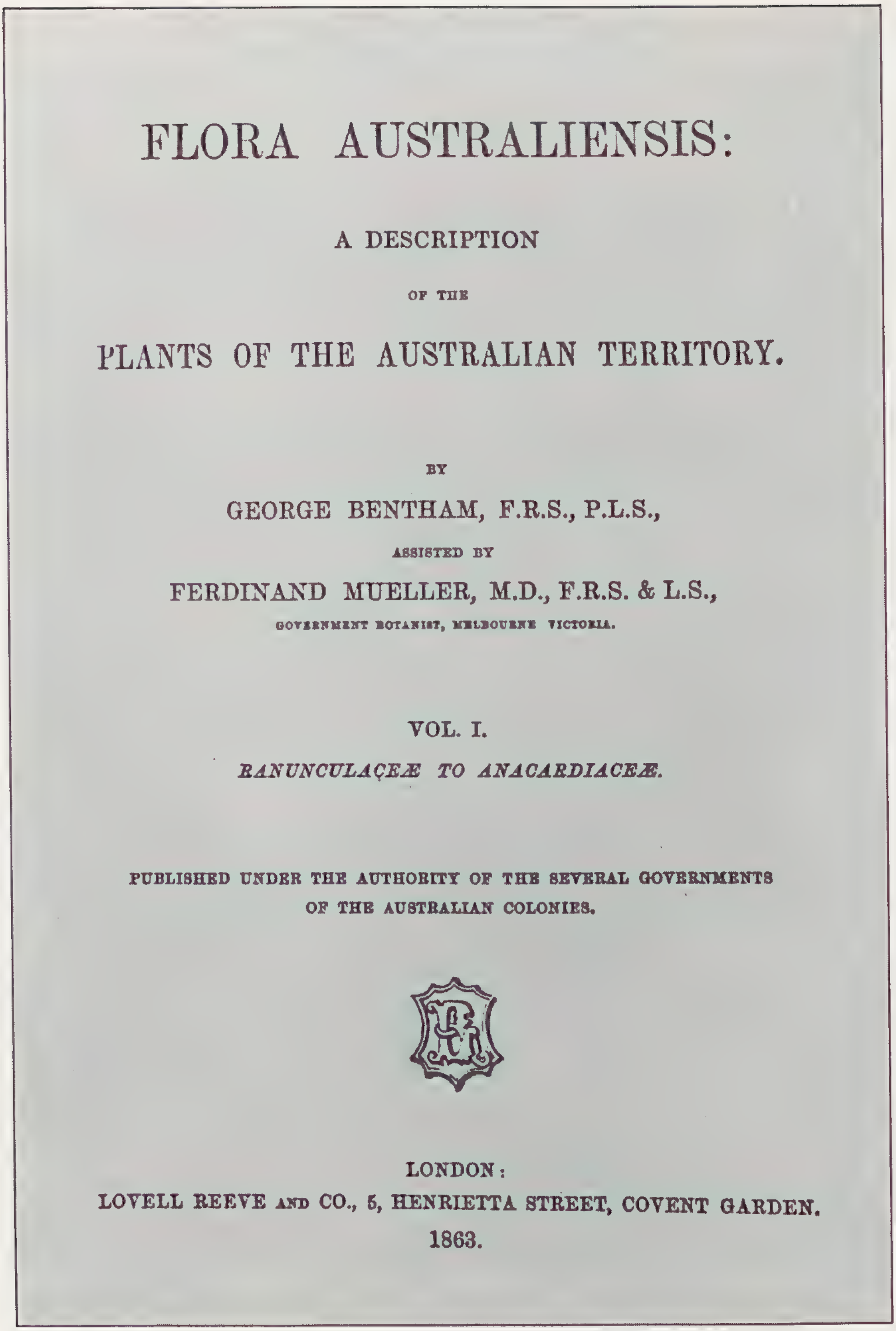
The project to write a *Flora of Australia* is the first of its kind in this country. Only one previous Australian Flora has been completed, *Flora Australiensis* (1863–1878), written by George Bentham who never visited Australia. The new *Flora* is the most exciting botanical project undertaken in Australia. It has had a long gestation and a difficult birth; its completion, like that of works such as de Candolle's great *Prodromus* (1823–1878) and Martius' *Flora Brasiliensis* (1840–1906), will be a major achievement of national and international co-operation.

Like all Floras, Bentham's *Flora Australiensis* was out of date as soon as the last volume was published. The seven volumes spanned 16 years, from 1863 to 1878, and were written entirely by George Bentham using the collections at Kew, the British Museum (Natural History) and Paris, as well as those sent on loan from Melbourne. During this period botanical work was expanding in Australia. Field collectors were active, many of whom were encouraged by Ferdinand Mueller, Government Botanist of Victoria. Mueller himself was in the heyday of a long and productive career. Botanists, both professional and amateur, were beginning to study the flora in other States. Bentham had planned a supplement but, in the preface to Volume 7 of *Flora Australiensis*, he wrote that it 'would entail more labour than at my age it would be prudent to undertake'; he was then 78. Instead, he encouraged Mueller to produce a complete census of the flora. Mueller accomplished this by 1882 and revised it in 1889.

State Floras, mostly based on *Flora Australiensis* with the addition of species discovered later, were issued over the succeeding years in all States except Western Australia, where a systematic census, prepared by the Government Botanist Charles Gardner, appeared in 1930–31. Most of these Floras were compiled by professional taxonomists appointed by State Governments or by universities. Because the botanists were few in number, demands on their time were such that they were often able to do little research. This problem, common to most botanists in Australia, is slowly being alleviated as more positions are created so that more people are available to share or assume routine responsibilities. By the 1900s, however, the first of many accomplished amateur taxonomists to contribute to the literature on the Australian flora had appeared on the scene. J. M. Black, a retired journalist, published *The Naturalised Flora of South Australia* in 1909, followed by his *Flora of South Australia* in 1922–29. The latter is currently in its third edition, revised by John Jessop, Chief Botanist of the State Herbarium of South Australia.

The first reference to a new national Flora appears to be that by Joseph Maiden, Government Botanist and Director of the Botanic Gardens, Sydney, in 1907. In his Presidential Address to Section D (Biology) at the eleventh meeting of the Australasian Association for the Advancement of Science, he suggested that each State issue supplements to *Flora Australiensis*, and went on to say:

> The form of the new 'Flora Australiensis' (which cannot be published until Western Australia is more thoroughly explored botanically) will then fitly take the form of the most modern classification available, which, at the present moment, is of course that of



FLORA AUSTRALIENSIS:

A DESCRIPTION

OF THE

PLANTS OF THE AUSTRALIAN TERRITORY.

BY

GEORGE BENTHAM, F.R.S., P.L.S.,

ASSISTED BY

FERDINAND MUELLER, M.D., F.R.S. & L.S.,

GOVERNMENT BOTANIST, MELBOURNE VICTORIA.

VOL. I.

RANUNCULACEÆ TO ANACARDIACEÆ.

PUBLISHED UNDER THE AUTHORITY OF THE SEVERAL GOVERNMENTS
OF THE AUSTRALIAN COLONIES.

LONDON:
LOVELL REEVE AND CO., 5, HENRIETTA STREET, COVENT GARDEN.
1863.

Figure 1. Titlepage of Volume 1 of George Bentham's *Flora Australiensis* (1863).

> Engler, although even that fine arrangement need not be slavishly followed in every detail.
>
> We in Australia suffer much through our geographical isolation from the great intellectual centres of the Northern Hemisphere. That is our misfortune, but we should not fail in our endeavors to advance knowledge of the botany of this continent, and potent help in this direction would be the issue of an 'Australian Flora' based on the most modern lines of taxonomic research, modified, indeed, by our own special knowledge of our own plants and their affinities.

Nine years later, however, Maiden acknowledged that a new Flora was some time off. In the preface to the *Census of New South Wales Plants* (1916), compiled jointly with Ernst Betche, he wrote that Bentham's *Flora Australiensis* 'is, and will long remain, the standard work on our flora. The greater one's experience with it, the more sincere is one's admiration of it'. This opinion has been echoed by most Australian taxonomists.

While the need for a new Flora was realised and occasionally mentioned, there seems to have been no attempt to fulfil that need during the first half of the 20th Century.

The period after the Second World War was a quiet one for the Flora proposal. The staff of botanical institutions were still preoccupied with routine work, preparation of State floras, and individual lines of research. With every year, however, the need became more urgent, yet still no firm action was taken.

At the 25th meeting of the Australian and New Zealand Association for the Advancement of Science (ANZAAS) in Adelaide, August 1946, a meeting of plant taxonomists recommended the formation of a Systematic Botany Committee. The meeting listed, under 'immediately desirable tasks', the 'preparation of floras, especially for some States'. Clearly there was no strong feeling about a national Flora. The Committee fostered communication among the taxonomic community by issuing a newsletter entitled the *Australasian Herbarium News*. In the first issue, of June 1947, William Hartley, then Senior Plant Introduction Officer with CSIRO, called for the establishment of a new Commonwealth Herbarium which could facilitate the preparation of a Flora (Hartley, 1947). He envisaged that the Flora would be prepared by many botanists from the States, with the Commonwealth Government funding replacement staff during their period of commitment.

William Hartley's appeal brought no positive response. The next meeting of ANZAAS, in Perth, August 1947, again urged progress with State floras. This attitude, as stated by Stanley Blake, a senior botanist with the Queensland Herbarium, persisted through subsequent meetings including the 31st at Melbourne in 1955, at which 'an attempt to do something more definite . . . met with little response' (Blake, 1960). The *Australasian Herbarium News*, during the eight years that it was published, carried no further reference to a Flora.

The initial impetus to the campaign which finally led to the current *Flora of Australia* came from a newcomer to the Australian botanical scene, Hansjoerg Eichler. In 1957, less than two years after arriving from Germany to take up the position of Keeper in the State Herbarium of South Australia, Eichler recommended that his staff be permitted to undertake Australia-wide revisions which could be used towards a new *Flora of Australia*. This was a major change in policy; previously all States had largely confined research within their borders. Joseph G. Wood, then Professor of Botany at the University of Adelaide and Chairman of the Handbooks Committee of the Flora and Fauna of South Australia, immediately took up the suggestion for a national Flora and had it placed on the agenda for the 33rd ANZAAS Congress, held in Adelaide in August 1958. This time the topic aroused extensive discussion, during which it became clear that opinion was divided on the level of detail that would be appropriate for a Flora. There was support on the one hand for a monographic approach, based on full revision of all groups, and on the other for a concise treatment based solely on existing published knowledge. Eichler proposed the creation of a central taxonomic unit with 10 botanists producing revisional studies for a Flora.

ANZAAS resolved to set up a Flora of Australia Committee 'to prepare estimates and detailed plans of the organization required for the preparation of a new Flora Australiensis'. Members of the Committee were R. T. M. Pescott (Convener), S. T. Blake, D. J. Carr, Hj. Eichler, L. A. S. Johnson, S. Smith-White and D. E. Symon. A meeting was held in Melbourne on 22–25 April 1959, at which Blake was elected Chairman. Following intensive debate, a report was prepared recommending that a monographic work be produced, to be called *Flora of Australia*. The Committee dismissed the concept of a Flora based only on existing published knowledge, as not serving 'any useful purpose' (Blake, 1960). The idea of a generic Flora was also rejected, first because it would hinder the preparation of a full Flora, and second, because the species should be better known before genera could be properly delimited. The report envisaged that the Flora would be produced over a period of about twenty years by a central organisation with a staff of fourteen taxonomists under the direction of an Editor-in-Chief. It suggested that the organisation might be at Canberra but that some of the taxonomists could be stationed at existing herbaria or universities.

The Committee estimated that the Australian flora contained over 15 000 species and that a monographic treatment would amount to 30 000 pages. The cost at 1959 rates was estimated at £70 000 ($140 000) per annum for salaries, £15 000 ($30 000) for equipment, an unspecified amount for 'normal running costs', and 'ample funds for field work and for travel within Australia and abroad'. The Committee, noting that at that time there were less than 20 workers in taxonomy in State and Commonwealth herbaria and about six in universities, of whom none could devote full time to their researches, stated that graduates would have to be trained, although the 'initial staff would consist largely of experienced taxonomists'.

The Committee's report was adopted by ANZAAS at the 34th Congress in Perth, August 1959. A delegation from ANZAAS in July 1960 presented the report to the Prime Minister's Department, which in turn referred it to the Australian Academy of Science. The Academy, recognising the need not only for a Flora but also for a similar study of the Australian fauna, recommended to the Prime Minister of the day, the Right Honourable R. G. Menzies, that a Museum of Australian Biology be established with the principal aims of conducting a biological survey of Australia and writing a 'comprehensive multi-volume Flora of Australia'. The Government at that time was unable to finance the museum, although it did not refute the need for such a development. Throughout the period leading to the final decision to proceed with a new Flora, the Academy continued to give strong support to the concept.

A facsimile edition of Bentham's *Flora Australiensis*, published by Asher and Reeve in 1967, drew international attention to the lack of a modern Flora (Stafleu, 1967). It also prompted John Beard, then Director of Kings Park and Botanic Garden, Perth, to suggest that a concise Flora be compiled along the lines of *Flora Europaea* (Beard, 1968). Beard considered that such a Flora could be written by a small group of botanists working in Canberra.

The 1960s saw great economic development in Australia, especially in agriculture, mining and industry. At the same time awareness of its effects on the environment became more widespread, leading to a great surge in concern for the natural environment. In the public and private sectors, the need for environmental surveys in both settled and remote areas placed great demand on the services of botanists and made even more apparent the lack of a national Flora. During the same period horticultural interest in the indigenous flora also increased markedly.

In April 1967 the Honorary General Secretary of ANZAAS wrote to the Prime Minister expressing regret at the lack of support for a new Flora and emphasising the importance of the project. The proposal was again referred to the Academy of Science which appointed a Flora and Fauna Committee to examine it.

While ANZAAS continued to promote the 'Flora of Australia' concept, the Zoological Subcommittee of the Academy's Flora and Fauna Committee in 1968 canvassed the various State museums and found general support for a Commonwealth biological survey. By that time, State herbaria also were willing to collaborate in producing a national Flora. The Flora and Fauna Committee released a report in October 1968 in which it proposed that an organisation, to be called a Biological Survey of Australia, be established (Anon., 1968). The report proposed that the Survey would initiate the production of a new Flora of Australia; it was still envisaged that the Flora would be monographic. The suggestion was made that existing herbaria in Canberra might form the basis of the botanical collections. At that time there were separate, small herbaria, in CSIRO, the Forest Research Institute, the Botanic Gardens and the Australian National University. The Committee considered that collaboration with herbaria in the States would be essential. Early in 1969 Sir Macfarlane Burnet, then President of the Academy, led a delegation to the then Minister for Education and Science, the Honourable J. M. Fraser, to press the claim for establishment of a Biological Survey of Australia.

In 1970 and 1971 events occurred that greatly stimulated discussion on a new Flora and led to the commencement of preliminary work for it. For the James Cook Bicentenary in 1970 William Stearn, a distinguished botanist with the British Museum (Natural History), was invited to address the Australian Academy of Science. During his address, Stearn referred to the conspicuous absence of a modern Australian Flora and to the urgent need to write one. He was later approached confidentially by Sir Maurice Mawby, a Fellow of the Academy, who discussed with him the possibility of raising private funds to help launch work on a new Flora. Stearn referred Sir Maurice to John Beard, then Director of the Royal Botanic Gardens, Sydney. Beard drew up a proposal for regional Floras to cover Australia in four phytogeographic regions—South-eastern, Tropical, Eremean and South-western; these Floras would be written in five years, possibly by staff in the various herbaria. Sir Maurice's offer to assist was conditional upon support for the project being received from both the Academy and the Australian botanical community.

In February 1971 a meeting was held in Canberra to discuss an Information Retrieval Base for the information on herbarium labels. The agenda included an item on possible actions to promote preparation of a new Flora of Australia. Beard presented to the meeting his proposal for regional floras and indicated that private funds might become available to begin the work. The presentation surprised most delegates since they had been unaware of these developments, but the meeting tentatively supported the proposal. Within weeks, however, alternative proposals were drawn up by groups of botanists in Adelaide, Canberra and Melbourne. The Adelaide group, headed by Eichler, circulated a questionnaire among Australian botanists to gauge opinion on several possible courses of action. From this there emerged general support for a preliminary work, an index of Australian plant names, which could be commenced with the funds likely to be made available as a result of Sir Maurice's initiative.

The 43rd ANZAAS Congress in Brisbane followed in May 1971, and the whole Flora subject was discussed. Three proposals were submitted to the Academy of

Science, for an Australian Plant Name Index, a Generic Flora of Australia, and a series of Handbooks for regions not covered by floristic works. The first would provide basic data for a new Flora, the second would be a valuable source of information on the flora as an expansion of the *Dictionary of Australian Plant Genera* (Burbidge, 1963), while the third would fill the gaps in the field of Australian regional floras.

The Academy in November 1971 set up a Standing Committee for a Flora of Australia under the chairmanship of David G. Catcheside, then Director, Research School of Biological Sciences, Australian National University. It consisted of an experienced, active taxonomist from each State and the Australian Capital Territory and six botanists from Australian universities. With general support from botanists for the Australian Plant Name Index, the Standing Committee decided to initiate the project, using the funds made available to the Academy through Sir Maurice Mawby. Nancy Burbidge was released from her duties as Curator of the CSIRO herbarium to lead the project, and Eichler took up the Curatorship. The Committee also discussed the format for a Flora and arranged the preparation of sample treatments. Thus important groundwork for a Flora was at last under way. Both the Academy and CSIRO had been instrumental in reaching this goal. The Academy continued to administer the project financially until 1976. CSIRO made available research and library facilities.

In May 1972 the Academy wrote to the then Minister for Education and Science, the Honourable J. M. Fraser, requesting reconsideration of the proposal to establish a Biological Survey. Further support for this proposal came in the same year from a House of Representatives Select Committee on Wildlife Conservation (Waterhouse, 1978).

During the 1970s active support for the project also came from an active amateur group, the Society for Growing Australian Plants. The Society, its members acutely aware of the need for accurate names and data on native plants used in horticulture, on several occasions urged the Government to begin writing the Flora.

The need for a biological survey had now become sufficiently important for the major Australian political parties to include it in their platforms for the Federal Election in 1972 (Ride, 1978). It seemed only a matter of time before the survey would be set up.

Communication and co-operation between Australian botanists received a boost with the formation in April 1973 of the Australian Systematic Botany Society. First proposed by a group of Victorian botanists, the Society rapidly gained a membership of over 200 and now (1981) has over 300 members. Local chapters were formed in the larger cities. The Society immediately began to play its part by preparing an index to current plant taxonomic research in Australia. In 1976 John Jessop, who had succeeded Eichler as head of the State Herbarium of South Australia, proposed that the Society co-ordinate and edit a *Flora of Central Australia*. Although there was concern that it might lessen support for a national Flora, the project went ahead, as it was felt that it could be completed before work on a national Flora commenced. Further, it was to be based primarily on published knowledge or that readily available from specialists. The *Flora of Central Australia* (Jessop, 1981), prepared by over 50 contributors in three years, covers a major geographical region of the continent but, with about 2 000 species, includes only ten per cent of the Australian flora. The project has played its part both in directing attention to the need for Floras and in giving many people experience in flora-writing.

A visit to Australia in 1973 by C. G. G. J. van Steenis, then Director of the Rijksherbarium, Leiden, focussed attention on the scope and organisation of flora-writing through discussion of *Flora Malesiana*. Van Steenis strongly preferred a concise flora, but some of the senior local voices still wanted a monographic work.

The *Australian Plant Name Index* project commenced in April 1973 with the appointment as bibliographer of Penelope Hack, who was succeeded in January 1974 by Arthur Chapman. Nancy Burbidge directed this work and at the same time brought up to date her earlier list of taxonomic literature available in Australian libraries (Burbidge, 1951, 1978). She also planned three sample treatments for a Flora text, to be made available for discussion. These were undertaken by herself (Loranthaceae), Helen Hewson (Brassicaceae), and Ruurd Hoogland (Rhizophoraceae).

In 1973 the Government established the Interim Council of the Australian Biological Resources Study (ABRS). The Council's functions were:

(a) Initially to promote through grants to existing State and Commonwealth institutions:
  - the collection and scientific description (taxonomy) of species of animals and plants throughout Australia;
  - in-depth studies of the ecology of such species; and
  - proper maintenance of collections.

(b) After a few years of operations, to consider and make recommendations in relation to:
  - conduct in the longer term of taxonomic and ecological studies; and
  - housing, maintenance and display of national scientific collections (Waterhouse, 1978).

The Council was allocated $750 000 for the first three years. On the botanical side grants were made for taxonomic and ecological studies and for the curation of collections.

A picture of the state of taxonomic knowledge of the Australian flora was built up, following an assessment by Nancy Burbidge in the early 1970s. Burbidge estimated that 25 families of seed plants were sufficiently well known to be written up for a Flora; 73 small families could also be written up without detailed research; 84 families required revision in most genera; 7 could be written up at a non-critical level; and 33 were of doubtful position (Burbidge, 1974). In 1978 a survey conducted by ABRS revealed that only 37 of the 222 flowering plant families recognised by Burbidge were being actively studied in Australian herbaria (Ride & McCusker, 1978). Although there was doubt as to the final format of the Flora, it was felt that a work based on current knowledge would quickly lose value and that a 'vigorous modern Bentham' was needed urgently to get on with the job (Ride, 1978).

The Interim Council of ABRS presented its report in 1975. The report was referred by the Government to an Administrative Review Committee and a Committee on Co-ordination of Support for the Collection of Data in the Flora and Fauna of Australia. The question of the location of ABRS within the Commonwealth Public Service was considered by the Science Task Force of the Royal Commission on Australian Government Administration. Recommendations from these committees were finally referred to the Interim Australian Science and Technology Council (ASTEC). Following the initial three-year operation of ABRS, its funding was continued in 1976–77, during which period the report of the Interim Council was passing through the above committees. In 1976 financial support for the Flora project, which up till then had been organised by Sir Maurice Mawby and the Australian Academy of Science, was exhausted. Following an approach by the Academy, the project was taken over by ABRS.

A note of frustration appeared in the report of the Systematic Botany Committee of ANZAAS in 1976: 'The time lost on the Flora project since concrete proposals for it were submitted in 1959 is of scientific concern: progress in all fields of botany dealing with Australian plants . . . is severely hampered by the inadequacy of taxonomic knowledge . . . and the lack of a comprehensive work in which modern knowledge is made readily available'.

Further groundwork for a Flora was undertaken in 1976 by Paul Wilson, Senior Botanist with the Western Australian Herbarium, while on secondment to ABRS. He prepared a set of Guidelines for Contributors to a Flora which were widely circulated for comment among Australian taxonomists. Although prepared for a Flora which would be published in family parts, the Guidelines nonetheless contributed significantly to the format eventually adopted.

In its report for 1976–77, the Interim ASTEC recommended the establishment of a new body, the Institute of Australian Flora and Fauna (IAFF), to 'support and co-ordinate publication of a systematic series of regional floral handbooks'. It recommended that existing ABRS staff be incorporated into the new Institute. ASTEC saw the initial role of the IAFF, in relation to flora, as one of ensuring consistency in regional Floras, preparing and co-ordinating index volumes, and supporting taxonomic studies and handbooks. This would pave the way for the writing of a more complete Flora when appropriate funds became available. A further entreaty to the Government to continue funding ABRS and to commence a Flora came in December 1977 from the Committee of Heads of the Australian Herbaria.

The question of a biological survey of Australia, including the preparation of a national Flora, had now been under scrutiny for two decades. As a result of its investigations the Government, in 1978, formally established the Australian Biological Resources Study within the Department of Science. The preparation and publication of co-ordinating works on the flora were stated objectives. The introduction of a program to write a new Flora of Australia now seemed assured, but its timing, scope and format were still to be decided. The ABRS Advisory Committee was appointed by the Minister for Science and held its first meeting on 6–8 March 1979. It decided to recommend that a start be made immediately on a concise *Flora of Australia*. The Committee felt that the time needed to prepare a monographic Flora was unacceptable; the work must be completed within 30 years, and planned so that groups in urgent need of revision could be studied before the relevant volumes were issued. The Committee's recommendation was accepted by the then Minister for Science, Senator the Honourable J. J. Webster, who announced the project on 24 April 1979. Meanwhile, the scope and format were discussed at length among the taxonomic community. Support for a monographic treatment waned as the enormous time-scale involved became more apparent. An alternative proposal envisaged the publication of reprints of revisions in a standard format so that they could be bound in volumes; such a scheme might have been considered more thoroughly had not the Advisory Committee decided to commence the concise *Flora*.

At its second meeting on 4–5 October 1979, the Advisory Committee decided that the *Flora* would be based largely on current knowledge and 'would be produced in such a way as to be readily updateable'. It decided that, if possible, some parts should be published in time for the XIII International Botanical Congress in Sydney, August 1981.

In October 1979 a Flora Study Group was appointed, later to become the Editorial Committee for the *Flora of Australia*, under the Chairmanship of Sir Rutherford Robertson, Chairman of the ABRS Advisory Committee and Vice-chairman of ASTEC. The Study Group wasted no time in determining the scope, arrangement and format of the *Flora*. The initial choice lay between issuing volumes or family parts. The Committee quickly decided in favour of volumes. Several systems of classification were considered, the use of a phylogenetic system being preferred to any other arrangement because it would provide a definite framework and prevent groups from being neglected. The system of Arthur J. Cronquist (Cronquist, 1981), then at a late stage of revision, was chosen for the *Flora*.

The final administrative step of consolidation came in November 1979, when the Bureau of Flora and Fauna was established as a Branch in the Environment Division of the Department of Science and the Environment. A year later, the Division was transferred to the new Department of Home Affairs and Environment.

Current state of knowledge of the Australian flora

The Australian flora is still far from being adequately known. *Flora Australiensis* contained 8 125 species of vascular plants. In 1981 the number in the vascular flora is unknown but estimated to be about 18 000 species; in addition there are several thousand non-vascular species. A further significant increase will result from taxonomic revisions and more thorough botanical exploration. A sample of genera and sections of genera that have been revised in Australia during the past 40 years shows that the average increase in species when such revisions are made is just under 50 per cent. The sample may not be representative in that workers may have selected genera known to contain large numbers of undescribed species, though it included revisions of genera in which few new species came to light, e.g. *Phebalium* (4 new species in a total of 45) and *Terminalia* (2 in 29).

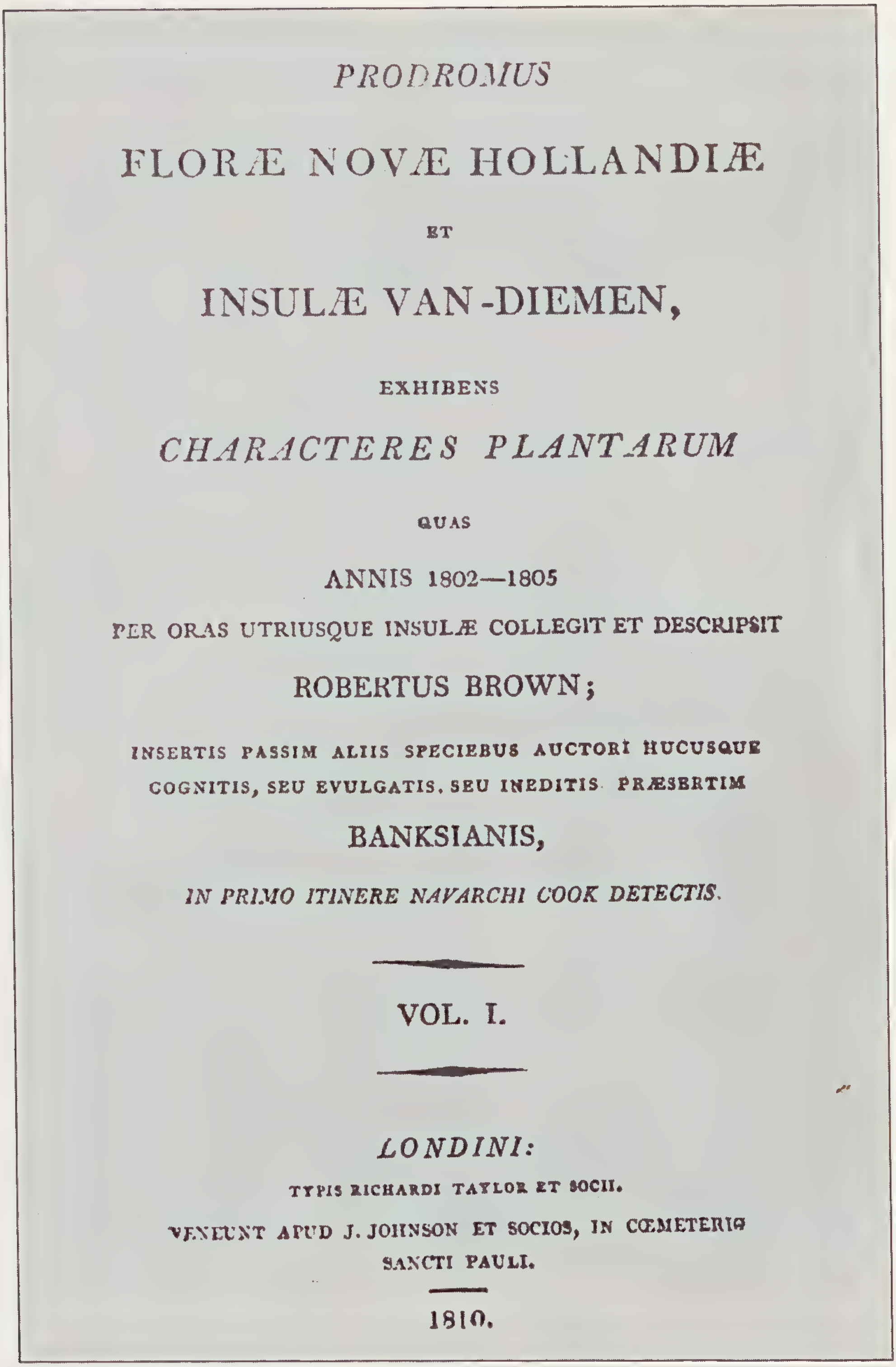
Few parts of Australia have been fully explored botanically. New species and records continue to be turned up, even close to civilisation, and there are very large areas—thousands of square kilometres—where no work at all has been done. This applies especially to parts of the north and to Western Australia. Collecting in such regions will in general extend the range of known species, but new discoveries are certain to be made. Alien taxa continue to become naturalised at a steady rate. In an analysis of the Victorian flora, for example, Ross (1976) calculated that the rate of introduction of non-Australian species to that State had averaged five to six species per year over the previous 100 years. There is little doubt that the Australian flora will eventually be found to contain over 25 000 species.

Previous floristic works on Australia

The first Australian plants named under the binomial system were two species published in 1768 by N. L. Burman. It was the large collection made by Joseph Banks and Daniel Solander in 1770, however, which gave the first real insight into the Australian flora. Unfortunately the *magnum opus* planned by Banks and Solander was never published, and their collections were only partly studied by other botanists. Banks encouraged and sometimes sponsored collectors to visit the continent, the most important of these being Robert Brown. Brown's participation in the coastal survey by Matthew Flinders in 1801–1803, and his subsequent stay in New South Wales and Tasmania, resulted in a collection of several thousand species. Brown commenced a Flora of Australia but the first volume, published in 1810 (*Prodromus Florae Novae Hollandiae et Insulae Van-Diemen*), was so disappointingly received that he never completed the remainder. The *Prodromus*, arranged in a natural system, later came to be recognised as a milestone in taxonomic botany.

Early works on the Australian flora were written and published in Europe, and many were largely accounts of individual collections, e.g. Labillardière (1804–1806) and J. D. Hooker (1855–1860) based chiefly on their own collections, and Lehmann (1844–1848) based on the collections of Ludwig Preiss and to some extent James Drummond (see Annotated Bibliography). The Royal Gardens (later Royal Botanic

Figure 2. Robert Brown (1773–1858), author of *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* (1810) and other works on the Australian flora. Painting by H. W. Pickersgill, engraved by C. Fox; reproduced by courtesy of the Linnean Society of New South Wales.



PRODROMUS

FLORÆ NOVÆ HOLLANDIÆ

ET

INSULÆ VAN-DIEMEN,

EXHIBENS

CHARACTERES PLANTARUM

QUAS

ANNIS 1802—1805

PER ORAS UTRIUSQUE INSULÆ COLLEGIT ET DESCRIPSIT

ROBERTUS BROWN;

INSERTIS PASSIM ALIIS SPECIEBUS AUCTORI HUCUSQUE
COGNITIS, SEU EVULGATIS, SEU INEDITIS PRÆSERTIM

BANKSIANIS,

IN PRIMO ITINERE NAVARCHI COOK DETECTIS.

VOL. I.

LONDINI:

TYPIS RICHARDI TAYLOR ET SOCII.

VENEUNT APUD J. JOHNSON ET SOCIOS, IN CŒMETERIO
SANCTI PAULI.

1810.

Figure 3. Titlepage of Robert Brown's *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* (1810).

Gardens) at Kew were associated with many early botanical collectors. By the 1850s Kew, under the direction of William Hooker, was becoming a major centre of botanical research. A series of colonial Floras was commenced there, *Flora Australiensis* (1863–1878) by George Bentham being an important contribution to this program. Ferdinand Mueller, the first resident plant taxonomist in Australia, had been keen to write an Australian Flora but was dissuaded by Bentham and Joseph Hooker. They considered that Mueller would be unable to do the work satisfactorily since he could not examine the historical collections housed in European herbaria. Mueller co-operated fully in the preparation of *Flora Australiensis* by making available to Bentham the entire collection of the herbarium in Melbourne (Daley, 1928).

As Government Botanist of Victoria from 1853 to 1896, Mueller developed the herbarium in that State into an institution of international importance. He encouraged collectors to travel to many parts of the continent; while he himself collected widely and produced a steady stream of taxonomic publications (for a bibliography of Mueller's works see Churchill, Muir & Sinkora, 1978). Mueller's botanical output has never been approached by later botanists in Australia. From his time onwards, however, the writing of floristic works on Australia has been carried out chiefly in this country, but with much reliance on the historical material in Europe.

Flora Australiensis spawned a number of regional floras, many of which were for the most part extracted from the major work. With time and the great increase in new discoveries, the original work necessary to compile Floras increased, as shown in works such as Black (1922–1929) and Ewart (1930). Floras were produced for all States except Western Australia; that State still has no Flora, though it has produced three censuses (Gardner, 1930–31; Beard, 1965; Green, 1981). Only South Australia, Tasmania, Victoria and the Australian Capital Territory have Floras that are either recent or kept up to date with new editions. There are modern local Floras for the Sydney Region, North-eastern New South Wales, Western New South Wales and Central Australia, and a Flora of South East Queensland is currently in preparation.

Annotated Bibliography

The following bibliography lists in chronological order the most significant floristic works that have been written for Australia and major regions within it. Several early taxonomic works of interest are also included. Publication years differing from those on title-pages are given in square brackets.

Burman, Nicolaas Laurens (1768), *Flora Indica*. Haak, Leiden & Schreuder, Amsterdam.

Contains the first two Australian plants named under the Linnaean system—both described as ferns attributed to Java, but in fact species of *Acacia* (Mimosaceae) and *Synaphea* (Proteaceae) from south western Australia.

Linnaeus, Carl (filius) (1781), *Supplementum Plantarum Systematis Vegetabilium, Generum Plantarum, et Specierum Plantarum*. Braunschweig.

Contains descriptions of several Australian plants seen by Linnaeus in Banks' herbarium.

Smith, James Edward (1793)[–1795], *A Specimen of the Botany of New Holland*. Davis, London.

Descriptions of plants collected at Sydney by early settlers, chiefly John White.

Figure 4. John Lindley (1799–1865), author of the names of many Australian plants. Portrait by J. H. Maguire, 1849; reproduced by courtesy of the Director, Royal Botanic Gardens, Kew.

Cavanilles, Antonio José (1800), Observaciones sobre el suelo, naturales y plantas del puerto Jackson y Bahía-Botánica, *Anales de Historia Natural* 1, 3: 181–245.

Descriptions of the plants collected at Sydney in March–April 1793 by Luis Née, a member of a Spanish expedition to the South Seas.

Labillardière, Jacques Julien Houtou de (1804–1806)[–1807], *Novae Hollandiae Plantarum Specimen*, 2 vols. Huzard, Paris.

Descriptions of plants collected by Labillardière and others in south-western Australia and Tasmania in 1792, arranged in the Linnaean sexual system.

Brown, Robert (1810), *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen*. Taylor, London.

The first Flora of Australia, albeit incomplete, based largely on the extensive collections made by Brown himself during the Flinders Voyage (1801–1803) and afterwards in New South Wales and Tasmania. Only one of two projected volumes published. One of the first major works to be based on a natural system.

Candolle, Augustin Pyramus de (et al.) [1824–](1823–1873), *Prodromus Systematis Naturalis Regni Vegetabilis*. Treuttel & Wurtz, Paris.

One of the greatest botanical works, intended to cover the flowering plants of the world but eventually included only the dicotyledons. The principles of nomenclature used in the work became the basis for the *International Code of Botanical Nomenclature*.

Lindley, John (1839–40), Sketch of the Vegetation of the Swan River Colony, Appendix to the first 23 volumes of *Edwards's Botanical Register*.

Descriptions of the plants collected by early settlers at the Swan River, Western Australia.

Lehmann, Johann Georg Christian (1844–1847)[–1848], *Plantae Preissianae sive Enumeratio Plantarum, quas in Australasia Occidentali et Meridionali-occidentali annis 1830–41 collegit Ludwig Preiss*. Meisner, Hamburg.

Almost a preliminary Flora of south west Western Australia, but without keys. Volume 2 also included many Drummond collections.

Hooker, Joseph Dalton (1855–1860)[–1859], *The Botany of the Antarctic Voyage of H.M. Discovery Ships 'Erebus' and 'Terror', in the Years 1839–1843, under the Command of Captain Sir James Clark Ross*, Vol. III, *Flora Tasmaniae*. Reeve, London.

The botanical results of the expedition's visit to Tasmania, together with an important essay on the Australian flora.

Harvey, William Henry (1858–1863), *Phycologia Australica, or a History of Australian Sea-weeds*, 5 vols. Reeve, London.

Colour plates and descriptions of the first major collections of Australian marine algae.

Mueller, Ferdinand Jacob Heinrich von (1858–1882), *Fragmenta Phytographiae Australiae*, Vols I–XII(part I).

A series containing descriptions of many new genera and species, comments on the status and relationships of many taxa, and notes on distribution.

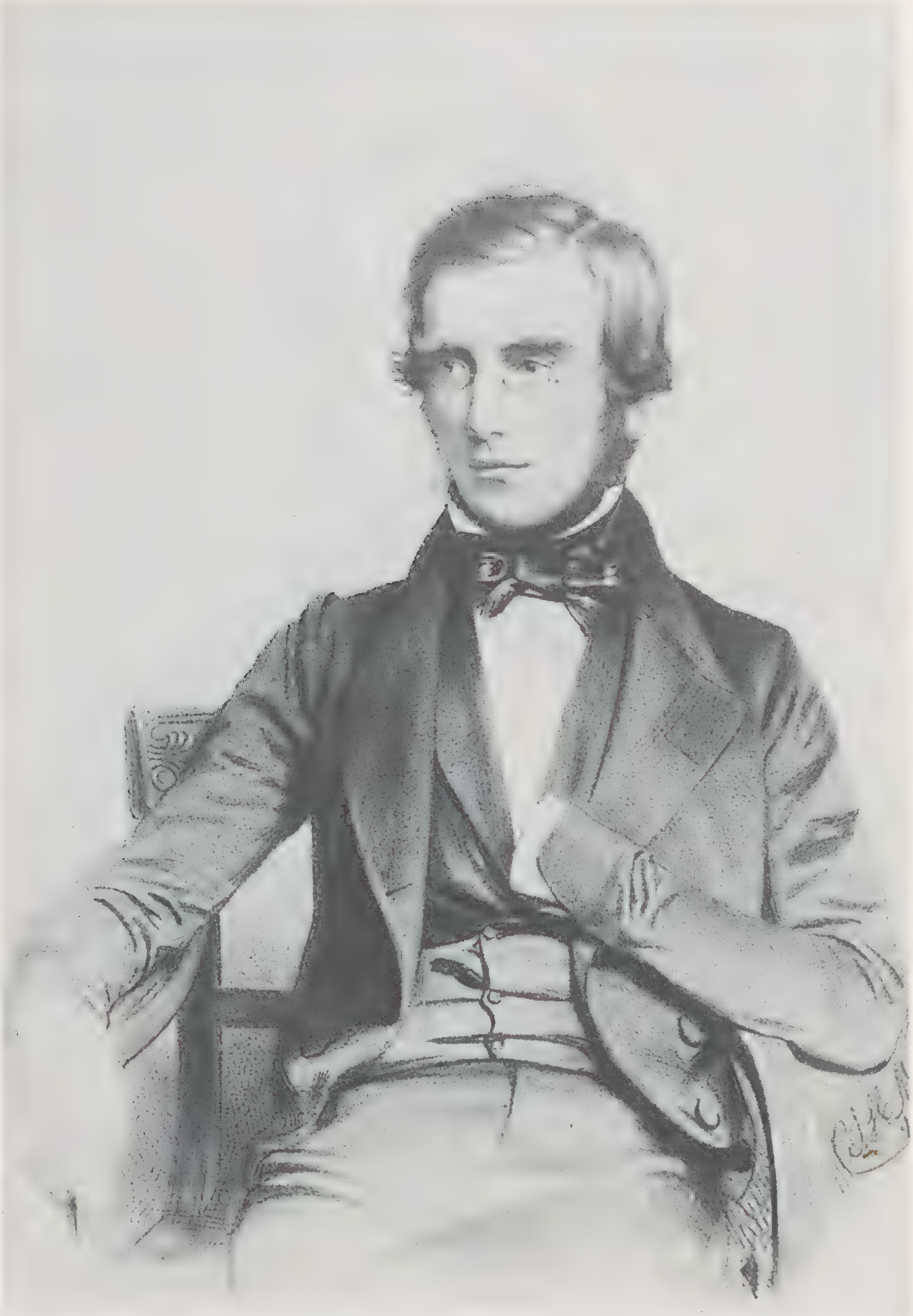


Figure 5. Joseph Dalton Hooker (1817–1911), author of *Flora Tasmaniae* (1855–1860) and of the names of many Australian plants. Portrait by J. H. Maguire, 1851; reproduced by courtesy of the Director, Royal Botanic Gardens, Kew.

Figure 6. Ferdinand Jacob Heinrich von Mueller (1825–1896), author of over one thousand papers and books on the Australian flora. Portrait from a photograph taken in 1865; reproduced by courtesy of the Director, Royal Botanic Gardens, Kew.

Mueller, Ferdinand Jacob Heinrich von [1862–](1860–1865), *The Plants Indigenous to the Colony of Victoria*, Vols I, II. Government Printer, Melbourne.

The first attempt at a State Flora in Australia.

Bentham, George (1863–1878), *Flora Australiensis: a Description of the Plants of the Australian Territory*. Reeve, London.

The standard Australian Flora for over a century.

Spicer, William Webb (1878), *A Handbook of the Plants of Tasmania*. Walch, Hobart.

A key to species, together with a systematic checklist and brief distributions, compiled by a clergyman. Arranged in the system of *Flora Australiensis*.

Woolls, William (1880), *Plants Indigenous in the Neighbourhood of Sydney*. Government Printer, Sydney.

A census of flowering plants and ferns with authorities, arranged in Mueller's system.

Tate, Ralph (1880), A census of the indigenous flowering plants and ferns of extratropical South Australia, *Transactions of the Royal Society of South Australia*, 3: 46–90.

A census with references to *Flora Australiensis* or Mueller's *Fragmenta*, and distribution in eight regions of the State. Arranged in Mueller's system. A supplement was issued in Vol. 4: 102–111 (1882).

Mueller, Ferdinand Jacob Heinrich von (1882), *Systematic Census of Australian Plants with Chronologic, Literary and Geographic Annotations*. Part I, *Vasculares*. Government Printer, Melbourne.

A census arranged in Mueller's own system which was based on Bentham's *Flora Australiensis*, together with original references, distribution by States, and the relevant references to *Flora Australiensis* and Mueller's *Fragmenta*.

Bailey, Frederick Manson (1883), *A Synopsis of the Queensland Flora, Containing both the Phaenogamous and Cryptogamous Plants*. Government Printer, Brisbane.

A very concise Flora, without keys, arranged in the Bentham and Hooker system and with a systematic index. Includes the ferns, mosses, lichens, fungi and algae, with family and generic descriptions and lists of species.

Mueller, Ferdinand Jacob Heinrich von [1886–](1885–1888), *Key to the System of Victorian Plants*, 2 parts. Government Printer, Melbourne.

Part I: A key with very short generic and specific diagnoses; includes a list of aliens.
Part II: A systematic list with distributions, illustrations.

Mueller, Ferdinand Jacob Heinrich von (1889), *Second Systematic Census of Australian Plants, with Chronologic, Literary and Geographic Annotations*, Part I, *Vasculares*. Government Printer, Melbourne.

A revision of the *Census* of 1882.

Tate, Ralph (1890), *A Handbook of the Flora of Extratropical South Australia, Containing the Flowering Plants and Ferns*. Education Dept., Adelaide.

An amplified key, covering 1 935 species, together with a list giving distributions. Arranged in the Bentham and Hooker system.

Moore, Charles & Ernst Betche (1893), *Handbook of the Flora of New South Wales.* Government Printer, Sydney.

Keys to families and genera, and amplified keys to species of flowering plants and ferns with brief generic descriptions. Based on Mueller's system.

McAlpine, Daniel (1895), *Systematic Arrangment of Australian Fungi, together with Host-Index and List of Works on the Subject.* Government Printer, Melbourne.

A census with original references, brief diagnoses, and distributions by States. Arranged in McAlpine's own system.

Bailey, Frederick Manson (1899–1902), *The Queensland Flora*, 6 vols. Diddams, Brisbane.

Based directly on *Flora Australiensis* with the addition of species described since that work and illustrations of some species. An index was issued in 1905.

Rodway, Leonard (1903), *The Tasmanian Flora*. Government Printer, Hobart.

A very concise Flora with many line drawings, covering 1 286 species (including aliens), based on the Bentham and Hooker system.

Diels, Ludwig & Ernst Pritzel (1904–1905), Fragmenta phytographiae Australiae Occidentalis, *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 35, 1: 55–662.

The results of extensive work in southern Western Australia, including the description of many new species.

Dixon, William A. (1906), *The Plants of New South Wales*. Angus & Robertson, Sydney.

Keys to families, genera and species of flowering plants and ferns, arranged in the Bentham and Hooker system.

Black, John McConnell (1909), *The Naturalised Flora of South Australia*. Privately published, Adelaide.

The first floristic work written in Australia on introduced plants, concisely covering 368 species with many line drawings. Arranged in the Bentham and Hooker system.

Ewart, Alfred James, assisted by James Richard Tovey (1909), *The Weeds, Poison Plants, and Naturalised Aliens of Victoria*. Government Printer, Melbourne.

Part I: described and discussed the more important poison plants and weeds; illustrated.
Part II: a census of 364 naturalised aliens and introduced exotics, with general distribution, country of origin and date of first record. Arranged in alphabetical order, but with a supplementary list of families arranged according to the Bentham and Hooker system.

Bailey, Frederick Manson (1909)[1913], *Comprehensive Catalogue of Queensland Plants, both Indigenous and Naturalised.* Government Printer, Brisbane.

A census with authorities and, for some species, supplementary notes; line and colour illustrations. Arranged in the Bentham and Hooker system.

Rodway, Leonard (1914–1916), *Tasmanian Bryophyta*, Vol. I, *Mosses*; Vol. II, *Hepatics*. The Royal Society of Tasmania. (First published as papers in *Papers and Proceedings of the Royal Society of Tasmania*).

Synopses of families and higher taxa; keys to species in genera with more than one species.

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THE AUSTRALIAN FLORA : ITS ORIGIN AND EVOLUTION

B. A. Barlow

The plants of Australia — a unique flora?

From the time of their first discovery and study by European naturalists, the plants of Australia have been noted for their uniqueness, almost as curiosities of the Earth's vegetation. This feeling is reflected by the very name, Botany Bay, of Captain James Cook's landing site of 1770 where Banks and Solander enthusiastically made the first intensive plant collection of the continent. For the next half-century or so, the pages of botanical journals such as Loddiges' *Botanical Cabinet* and Curtis's *Botanical Magazine* were dominated by descriptions of strange new plants introduced into cultivation from New Holland. Even today the seemingly unusual features of the Australian flora are promoted, especially for the purposes of national and international tourism.

The 'uniqueness' of the Australian flora is of course a matter of interpretation. The flora is certainly unique in the sense that a very high proportion of its species are endemic to the continent. It is also distinguished by the fact that two large genera, *Eucalyptus* and *Acacia*, between them dominate almost all the plant associations of the continent. *Eucalyptus* has a very limited natural occurrence outside Australia, and most of the *Acacia* species in Australia belong to the phyllodinous group which is also almost confined to the region. In a broad sense, then, the special character or uniqueness of the Australian flora is generally expressed in terms of plant communities dominated by *Eucalyptus* and *Acacia*, and including other genera and species which do not occur anywhere else.

At a higher taxonomic level the uniqueness of the Australian flora virtually disappears. Almost all the angiosperm families in Australia occur widely elsewhere. Conversely, almost all the larger families of the world occur in Australia. In this sense, the Australian flora is simply a typical part of the world flora and the special character of Australian plants at lower taxonomic levels has to be explained in terms of the geographical and climatic conditions under which the continental flora has developed.

The early phytogeographers, floristic 'elements', and the invasion theory

A century of J. D. Hooker

It is not surprising that the recognition of a unique character in the Australian flora quickly led to questions and speculation on the origin of the flora. Since Australia is an island continent, how did this remarkable flora get here? Where did it come from, and when? The first major work on this topic, which provided the prime impetus for theories on the origin and evolution of the flora for a century to follow, nearly coincided, in fact, with the long-awaited publication of Darwin's *Origin of Species*. This work, by the eminent English botanist J. D. Hooker, took the form of an introductory essay to a Flora of Tasmania (Hooker, 1860). Hooker had an excellent general knowledge of the entire world flora, and had already acquired a detailed knowledge of the floras of India and Africa. In the introductory essay he analysed the floristic records not just of Tasmania, but of the whole of Australia. He integrated the unpublished records known to him with the published ones in a classical phytogeographical analysis in which the Australian flora was broken down into 'elements' based on taxonomic affinities with the floras of other regions. For example, Hooker pointed out that many Indian plant genera were represented in northern Australia, in comparable monsoon habitats, and that Malaysian rainforest genera were represented in the appropriate habitats of tropical eastern Australia. In temperate south-eastern Australia he recognised that the floras of cool rainforest and alpine habitats shared genera with both New Zealand and temperate South America. At the family level, he noted common representation in the floras of south-western Australia and South Africa.

Hooker thus identified three elements in the Australian flora, and it is not surprising that there is a strong ecological as well as taxonomic distinction between them. These were (1) an autochthonous (Australian) element consisting mainly of endemic or almost endemic taxa occupying temperate open forest, woodland and heath habitats and mainly xeromorphic in character, (2) an Indomalayan element represented in tropical and subtropical rainforest and monsoon habitats and showing taxonomic affinity with plants of similar habitats in the Indomalayan region, and (3) an Antarctic element represented in temperate rainforest and alpine habitats, characterised by *Nothofagus* and showing taxonomic affinity with plants of New Zealand and temperate South America in particular. Hooker also noted the presence of cosmopolitan plant groups, mostly herbaceous, and widely distributed within Australia. It can hardly be said that Hooker drew any firm conclusions as to the actual history of the Australian flora, but his phytogeographical analysis was certainly the basis of the theory generally accepted for the next century. This theory was based on the concept of colonisation of the Australian land mass by separate invasions of different floras, perhaps at different times.

The 'invasion' theory depended on several assumptions. First, it was assumed that the earth's geography was fixed, so that Australia's position relative to other continental land masses had not changed. It was noted, however, that changes in sea level and/or tectonic movements in the earth's crust could have created land bridges between Australia and other regions. Secondly, it was recognised, from the comparable plant associations in Australia and elsewhere, that whole plant communities had migrated together. In fact, there was relatively strong resistance to the idea of individual plant migration through long-distance dispersal. Thirdly, it was assumed that the flowering plants could not have arisen in Australia, and must therefore have been established in Australia as colonisers from outside. Reasons for this belief were rarely given, and one suspects that it may simply have been concluded that Australia was too insignificant a place to have been the ancestral home of the angiosperms.

The invasion theory for the origin of the Australian flora was compatible in some respects with the theories of the time for the origin of the Australian vertebrate fauna, dominated as it is by marsupials. The theories thus gained some strength from mutual support. For plants, the invasion theory was generally developed along the following lines.

The first angiosperm colonisers probably entered Australia in Cretaceous times (see Table 2). The fossil record showed that even though this may have been relatively early in the history of the angiosperms, the major flowering plant families had already differentiated. During this time Australia was connected to Asia by a much more extensive land bridge across what is now the Indonesian Archipelago, and the first angiosperm invasion probably came, therefore, from the north-west.

The Indomalayan land bridge was thought to have broken up at the end of the Cretaceous period, over 50 million years ago (50 m.y. BP), leaving the Australian angiosperm flora of the time to evolve in isolation. Since the previous vegetation of the continent consisted of gymnosperms and lower land plants, the first angiosperm flora probably evolved under conditions of low competition, and therefore of low selection pressure, and underwent a period of rapid evolutionary diversification to occupy the broad spectrum of available habitats. Radiation in isolation thus gave rise to the diverse and unique autochthonous element with its high endemism. The autochthonous element came to be thought of as the oldest component of the Australian flora, and has been commonly referred to as the Palaeoaustralian element by biogeographers of the 20th century.

The Indomalayan and Antarctic (or Subantarctic) elements were thought of as the results of later angiosperm invasions of the region. The later invaders would have encountered an established and adapted angiosperm flora, and would have been confined by competition to habitats to which they were already well adapted. These two elements have thus persisted with much less change and, as a consequence, show a more obvious taxonomic affinity with their ancestral floras in other areas. The Indomalayan element was of course seen as the result of a later migration from the tropical north and west, perhaps over the same land bridge as existed for the first invasion. The Antarctic element was thought to have arrived over a land bridge from the south-east, perhaps now represented by the South Tasman Ridge and Macquarie Rise, at a time when Antarctica was free of an ice-cap and extensively vegetated by a southern temperate flora.

This interpretation of the history and relationships of the Australian flora was followed, in whole or in part, by a succession of authors. Tate (1888) applied it particularly to an analysis of the arid zone flora. Diels (1906), who had collected in Western Australia under the sponsorship of Engler, developed this approach rather precisely and concluded that the South West Botanical Province of Western Australia was the centre of origin of the Australian element. Perhaps the first author who seriously attempted to correlate botanical and geological histories of the Australian region, however, was Andrews (1916), who accepted the phytogeographical divisions of the flora and was the first to suggest that soil properties may have a bearing on distribution of Australian floristic elements. He suggested that scleromorphy, which characterises much of the Australian element, was an adaptive response to low levels of soil nitrogen and calcium. This idea has been extended by a number of later authors and is further discussed below.

Schwarz (1928) produced a phytogeographical analysis of the northern Australian flora and recognised most of the elements accepted by earlier authors with the exception of the Antarctic element. Like Hooker (1860), he drew attention to the close similarity at the generic and even specific level of some plant associations of India and northern Australia. This similarity has subsequently been documented by Specht (1958) and has assumed an important place in current biogeographical theories (see below).

The integration of soil and climatic data with plant distribution and evolution was further developed by Crocker and Wood (1947). Their attention, however, was focussed on the Australian element, its Tertiary history and the Recent cycles of aridity which have influenced the evolution and distribution of an arid zone flora. This topic is also discussed in more detail below.

The phytogeographically-based invasion theory culminated in the monumental work of Burbidge (1960) on the phytogeography of the Australian region. As a result of her very detailed analysis of the floristic composition of Australia's major vegetation zones, she accepted the idea of distinct floristic elements. She accepted that the autochthonous element may have been derived from an immigrant flora although she suggested alternatively that it may have 'developed from a pre- or early Cretaceous (Australian) flora of an unknown type'. She described north-east Queensland and Tasmania as important 'portals' for the Indomalayan and Antarctic elements respectively. While she accepted the idea of a later invasion of an Indomalayan flora from the north, and of an Antarctic element from the south, she did express doubts about the existence of a former land bridge southwards from Australia.

The impact of the Smith-White school of karyoevolution

The prolific and pioneering karyological studies of Smith-White (1948a, 1948b, 1950, 1954a, 1954b, 1955, 1959) generated theories of genomic evolution which made a major contribution to the invasion theory. His work covered major families of the flora, and particularly of the Australian element, including Myrtaceae, Rutaceae and Epacridaceae. Contemporary studies by Smith-White's students extended to Proteaceae (Ramsay, 1963), Casuarinaceae (Barlow, 1959), Goodeniaceae (Peacock, 1963), Loranthaceae (Barlow, 1963) and Lobeliaceae (James, 1963). At that time Smith-White accepted the idea that the angiosperms originated outside Australia, and that the Australian flora was derived from a number of immigrant stocks. He strongly supported the ideas that an ancient palaeoaustralian element had evolved in isolation under conditions of low selection pressure, and that the Indomalayan element was derived from a later immigration from the north. He was less inclined to accept the idea of a major Antarctic element, and particularly of an Antarctic land bridge, but did postulate that the alpine flora was derived partly by long-distance dispersal from South America and Antarctica.

In support of this theory, Smith-White (see especially 1954b, 1959) drew attention to recurring patterns of chromosome number variation in several of the families mentioned. In the woody families Myrtaceae, Rutaceae, Proteaceae, Epacridaceae and Casuarinaceae, and to a lesser extent in the herbaceous families Goodeniaceae and Lobeliaceae, he pointed out that groups which were endemic to Australia, or nearly so, exhibited considerable diversity in basic haploid chromosome number when compared with related groups distributed beyond the Australian region. The situation in families Myrtaceae and Rutaceae is summarised in Table 1. The patterns of change in different families were different, but it was generally found that different basic haploid numbers characterised genera rather than species. Within genera (or comparable supra-specific groups) basic numbers were usually constant but polyploidy occurred, rarely in the case of some woody families and frequently in the herbaceous ones.

Smith-White (1954b, 1959; see also review by James, 1981) thus postulated that in the evolution of these families an early genomic instability was later replaced by an extreme stability. Following the initial angiosperm radiation, outside Australia, in which the chromosome numbers of the various angiosperm families were established, there was a secondary cycle of change in the differentiating palaeoaustralian element after the first angiosperm colonisation of Australia. In this phase of expansion, under conditions of low competition and reduced selection pressures, 'genetic experiments, including experiments in structural change and chromosome number' would have been favoured. The karyological data were thus consistent with the phytogeographical theory for the origin of a palaeoaustralian element. During later phases in the history of the flora, including the entry of the Indomalayan element and the evolutionary responses to Tertiary climatic changes, only a third-order cycle of genomic evolution would have been possible. In this phase, under conditions of strong competition and high selection pressures, drastic genomic rearrangements were not tolerated and genomic evolution was limited mainly to euploid changes, within established genera, on basic chromosome numbers which were now fixed.

This mass of consistent karyological data undoubtedly supported the invasion theory at a time when emerging geophysical data were starting to cast greater and greater doubts upon it. The subsequent collapse of the three-element, three-invasion theory was thus a rather dramatic event in the history of phytogeography in Australia. It is noteworthy that a relatively simple reinterpretation of the karyological data, in terms of current principles of population genetics and by the original authors of the data, now adds an important element of detail to current ideas on the origin of the Australian flora.

The challenge to the invasion theory

There seems to have been little opposition, among the earlier phytogeographers, to the three-element invasion theory. Gardner (1944) opposed it only in the sense that floristic elements could not be distinguished at the family level. It seems that only Herbert (1932, 1935, 1950, 1960, 1964, 1967) consistently denied the theory on floristic and ecological grounds, although he was supported in part by Beadle (1966). Herbert argued the existence of an ancient palaeotropical flora which was already established in Australia at least as far back in time as the early Mesozoic. Through comparisons between modern plant associations, in respect of distribution and composition, he argued that floristic 'elements' were merely the result of climatic and edaphic 'sifting' of the ancestral flora. He strongly opposed the idea of migration

Table 1. Distribution of chromosome numbers in the Myrtaceae and Rutaceae (modified from Smith-White, 1959), shown as number of species for subfamilies, tribes and subtribes. Asterisks (*) indicate groups endemic to Australia or nearly so.

	Gametic chromosome number													
	6	7	8	9	10	11	12	13	14	16 32	17	18 27 36 54	19	22 44
MYRTACEAE														
Chamelaucoideae Chamelaucinae*	15	1	5	9		10				1		2		1
Other Chamelaucoideae						4								
Leptospermoideae						89								7
Myrtoideae						6								6
RUTACEAE														
Rutoideae Boronieae*		2	2	10		5	1	2	12	19	1	15	2	
Other Rutoideae				2								11		
Aurantoideae				44								14		
Flindersioideae				4								2		

across land bridges, pointing out the need for suitable habitats within the bridge for migrating species and emphasising the sifting effect which such bridges would have on community structure. The current theories of Australian biogeography to some extent vindicate Herbert's views.

The main weakness in the invasion theory was of course the lack of geophysical evidence for the required land bridges. A Cretaceous land connection between Australia and south-east Asia was hypothetical, supported primarily by the existence of the present-day Indonesian Archipelago. The only evidence for an Antarctic bridge was the presence of submarine rises to the south and east of Australia, but there is nevertheless a broad gap of deep ocean between Australia and Antarctica. The other problem, discussed in more detail below, was that the fossil record of angiosperms in Australia, meagre though it was, produced no evidence that the autochthonous element was older than the Indomalayan or Antarctic. Assemblages containing plants of the latter stocks were recorded from widely dispersed sites in Australia extending back in time to the early Tertiary period, thus tending to support the idea of an ancient mosaic of vegetation as Herbert had envisaged it.

Plate tectonics and biogeography

Continental displacement and its implications

Continental displacement (continental drift) has existed as a valid explanation of world vegetation patterns for some time, and was preferred by such plant geographers as Cain (1944) and Good (1947). On theoretical grounds these authors were strongly opposed to long-distance dispersal and were attracted to the idea that whole floras could be exchanged across united continental masses. Nevertheless the theory remained in general disfavour primarily because it involved an element of circular reasoning in that the main supporting arguments came from plant distributions. More recently, discoveries of mid-ocean ridges, sea-floor spreading and palaeomagnetism have provided a geophysical basis for the lateral displacement of continental plates and have led to a ready acceptance of the theory of plate tectonics in biogeographical analysis.

For a land mass like Australia, which is relatively isolated geographically, the implications of continental displacement are very great. An immediate explanation is apparent, for example, for the existence of closely similar plant communities, with identical ecological relationships, in regions now separated by large ocean barriers. We can explain how a tree genus can occur in widely disjunct regions with the same genera of understorey plants in both regions, and with the same genera of parasites and predators. There is a general consensus that the current theory for the origin of the Australian flora, with its supporting evidence from the fossil record and from palaeoclimatic data, is quite consistent with the current models, from purely geophysical data, of the geographical history of the continental masses.

A brief account of the physical basis and biological consequences of continental displacement is given below, as a preamble to a general account of current theory on the origin of the Australian flora.

The theory of plate tectonics

The theory of plate tectonics, which forms the basis of all palaeogeography and of most modern biogeography, is quite simple and now lies very much in the realm of popular science. Its basis is the observation that earthquakes occur mostly in linear zones on the earth's surface, and that these zones enclose areas in which earthquakes do not occur. The aseismic regions of the earth's crust are called plates, and it is now known that it is the relative motion between these plates which causes deformation and earthquakes at their margins. A single plate often comprises both oceanic and continental regions, and the earth's surface is entirely covered by crustal plates in motion relative to each other.

There are three types of plate boundary. First, two plates may be moving apart. Material from below the crust upwells, often as massive outpourings of lava, and adds to the margins of the plates forming a ridge of young crustal material. Secondly, two plates may be colliding, in which case one plate may be thrust under the other, forming a deep trench, with the crustal material sinking back into the earth's mantle. Thirdly, two plates may slide past each other without formation or destruction of plate material, forming transform faults. Folded mountain belts parallel with the margins of plates are often the results of collisions, or simply 'bow waves' of continental movement.

The consequence of these processes is that through geological time the relative positions of the continents have changed as their plates have moved. In particular, there is evidence that at one or more times in the past the continents have been grouped into one or two supercontinents, and that these stages have been followed by rifting and separation of entire continental masses. Complementary evidence is available from a number of sources, including matching of continental margins and mid-ocean ridges, tracing of polar wandering paths from palaeomagnetic studies, and the actual measurement of the rate of new crust formation.

Geography of the past

There is now general agreement on Australian palaeogeography, with current studies mainly resolving questions of detail. In the Jurassic (see Table 2) the southern supercontinent comprised what are now South America, Africa, Madagascar, India, Australia, Antarctica and New Zealand (Fig. 7). Rifting began in the middle/late Mesozoic with a separation of South America and Africa, progressing from north to south. Other relatively early separations included Madagascar and India, and also the late Cretaceous separation from Australia of New Zealand and the Lord Howe Rise. By early Tertiary time the southern lands may have had a configuration like that shown in Fig. 8, with Australia still joined to Antarctica on a broad front, and South America and Antarctica retaining their narrow connection.

Possible geographical relationships between Australia and Antarctica during the Tertiary period are illustrated by Crook (1981) and Kemp (1978, 1981). Rifting was initiated in the Palaeocene (Fig. 9), and by the middle Eocene had formed a wide gulf opening westwards (Fig. 10). Crook (1981) suggested that the first opening was a narrow seaway which completely separated the two land masses except for a possible residual contact at the south-western corner of Australia. A more widely accepted view, however, is that Australia and Antarctica remained joined by the South Tasman Rise (Fig. 10), and that the connection probably persisted until late Oligocene time, when Australia was entering lower latitudes (Figs 11, 12). The narrow land connection between South America and Antarctica was also maintained at least until this time (Jardine & McKenzie, 1972).

The northward movement of Australia continued through Miocene time (Fig. 13), and subsequently, at rates as high as 7.4 cm per year (Weissel & Hayes, 1974). The northern margin of the Australian Plate at that time was formed by what is now southern New Guinea. In the mid-Miocene, about 15 m.y. BP, the Australian Plate came into contact with the Sunda island arc system, forming the present New Guinean land mass and possibly also creating a relatively continuous land connection with south-east Asia (see page 46 for further details). The continued northward movement

ERA	PERIOD	APPROX. AGE (10^6 YRS)	EPOCH			STAGE	
CAINOZOIC	QUAT.		PLEISTOCENE				
	TERTIARY	2.5	NEOGENE	PLIOCENE			
		10		MIOCENE			
		27	PALAEOGENE	OLIGOCENE			
		38		EOCENE			
		54		PALAEOCENE			
MESOZOIC	CRETACEOUS	65	UPPER		65	SENONIAN	Maastrichtian
					70		Campanian
					80		Santonian
					85		Coniacian
					90		Turonian
					100		Cenomanian
		110	LOWER		110		Albian
					122		Aptian
					125	NEOCOMIAN	Barremian
					127		Hauterivian
					130		Valanginian
					132		Ryazanian
	JURA.	135			135		Tithonian

Table 2. Geological time scale since the Jurassic. (After Raven & Axelrod, 1974; reproduced by permission from *Ann. Missouri Bot. Gard.* 61: 559)

of the Australian plate has subsequently produced a disjunction from the Sundaland plate (Specht, 1981c), recreating an ocean barrier between the two.

Climates of the past

Palaeoclimates have been determined partly by palaeogeography and partly by the global climate, particularly the extent of polar ice-caps (Kemp, 1978). There is an element of circularity in the procedure for measuring palaeoclimates in the sense that palaeotemperatures, which are used to explain plant distribution, are determined from analysis of fossils, but these palaeotemperature data are determined mainly from oxygen-isotopic analysis of planktonic foraminifera and refer to the sea surface and bottom temperatures. They are thus remote from terrestrial fossil data, yet they do have considerable bearing on the interpretation of terrestrial palaeoclimates.

At the beginning of the Tertiary period, seas in high latitudes were much warmer than they are now, perhaps with surface temperatures of 18–20°C at latitudes higher than 60°S (Kemp, 1978). There is no evidence of an ice-cap on Antarctica at that time. The polar high pressure system would have been much reduced in intensity and extent, and a broad zone of westerly winds would have influenced southern Australia (Fig. 9). Further north, weak and erratic circulation patterns associated with warm sea surfaces would have resulted in deep inland penetration by rain-bearing winds. These conditions may have persisted through the Eocene, with water temperatures on the Campbell Plateau dropping from 20°C to 10°C and some glacial activity being

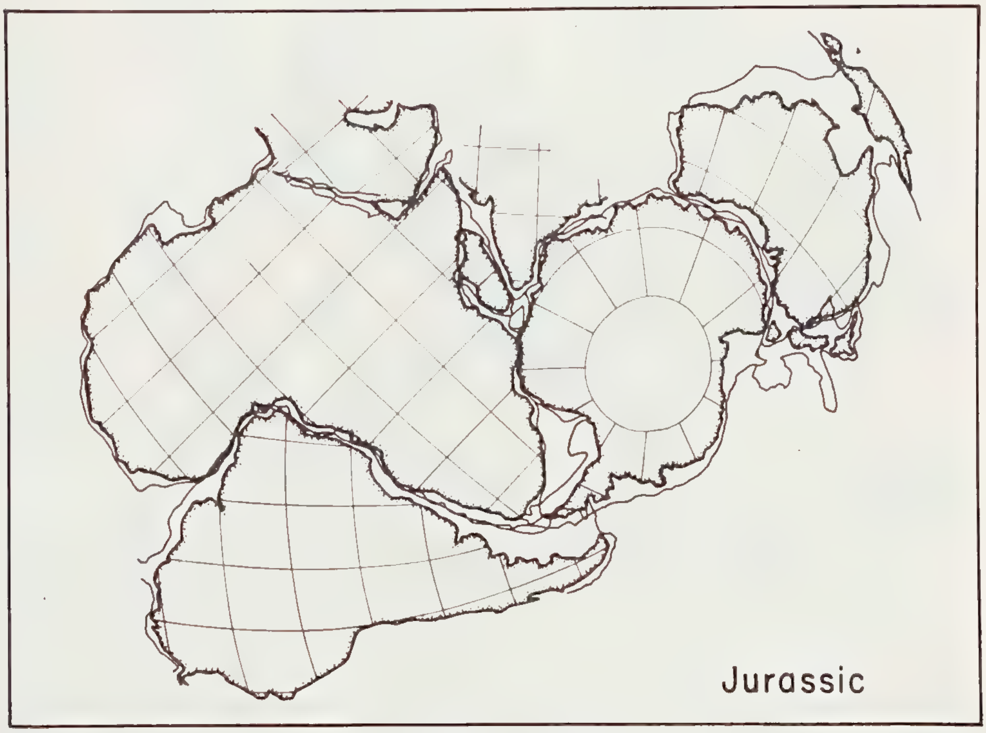


Figure 7. Fit of the Gondwana continents during the Jurassic, prior to breakup. (From Raven & Axelrod, 1974, after Smith & Hallam, 1970; reprinted by permission from *Ann. Missouri Bot. Gard.* 61: 540)

initiated in Antarctica (Fig. 10). However even these conditions were warmer than those of the present. The lowering of temperatures would have been associated with a lowering of precipitation.

The final separation of Australia and Antarctica in the Oligocene initiated circumpolar oceanic circulation, reducing heat transport from equator to pole and increasing the temperature gradient between those regions (Kemp, 1978). Sea surface temperature of the Campbell Plateau dropped to 6–7°C and probably nearly to freezing near Antarctica. The westerly wind systems would have extended further northwards as a result of these developments (Figs 11, 12). A simple explanation of the influence of conditions in Antarctica on the climate of Australia is given by Kemp (1981).

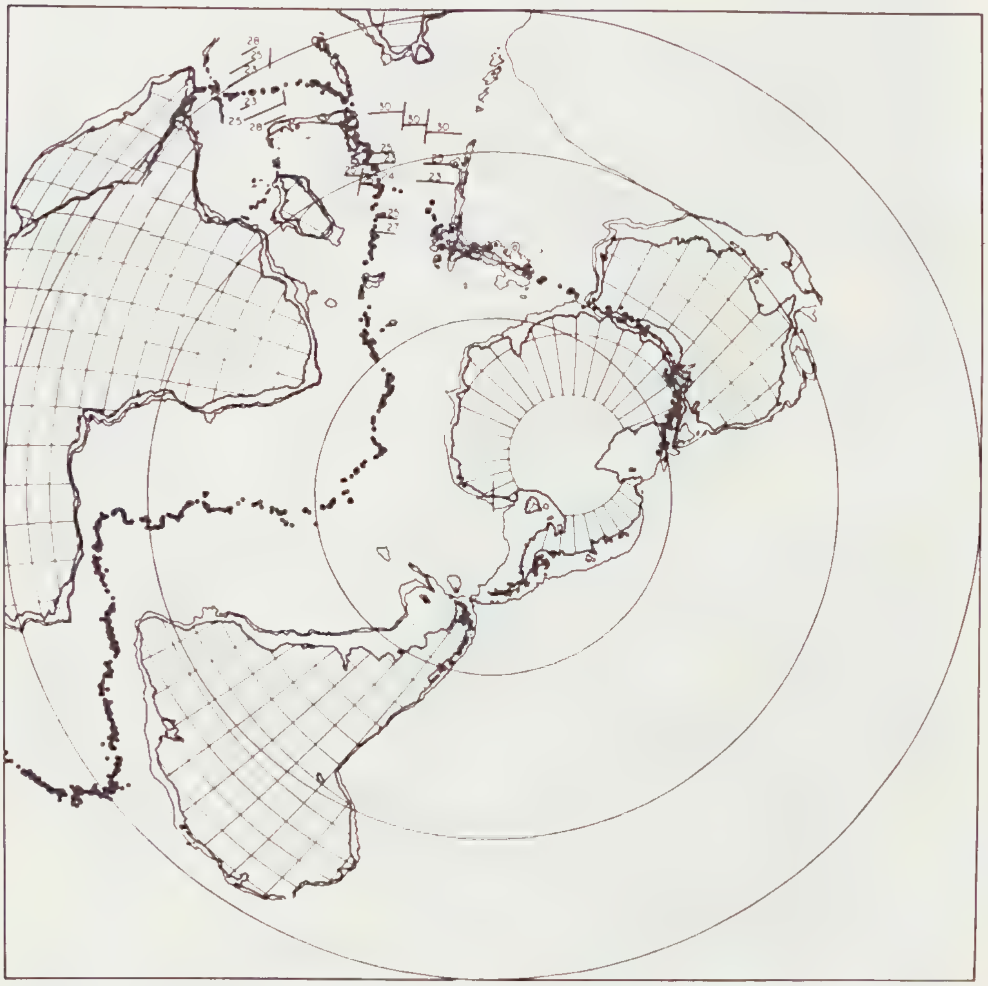


Figure 8. Reconstruction showing early Tertiary configuration of Gondwanan continents. Dots show active plate boundaries at that time. (From Jardine & McKenzie, 1972; reprinted by permission from *Nature* 235: 22. © 1972, Macmillan Journals Ltd.)

Figure 9. Palaeogeographical reconstruction of the Australian region for the middle Palaeocene (58 m.y. BP), with tentative atmospheric palaeocirculation indicated by heavy arrows. Shallow seas transgressing the present continental margin are shown in stipple. (From Kemp, 1978; reprinted by permission from *Palaeogeography, Palaeoclimatology, Palaeoecology,* 24: 180)

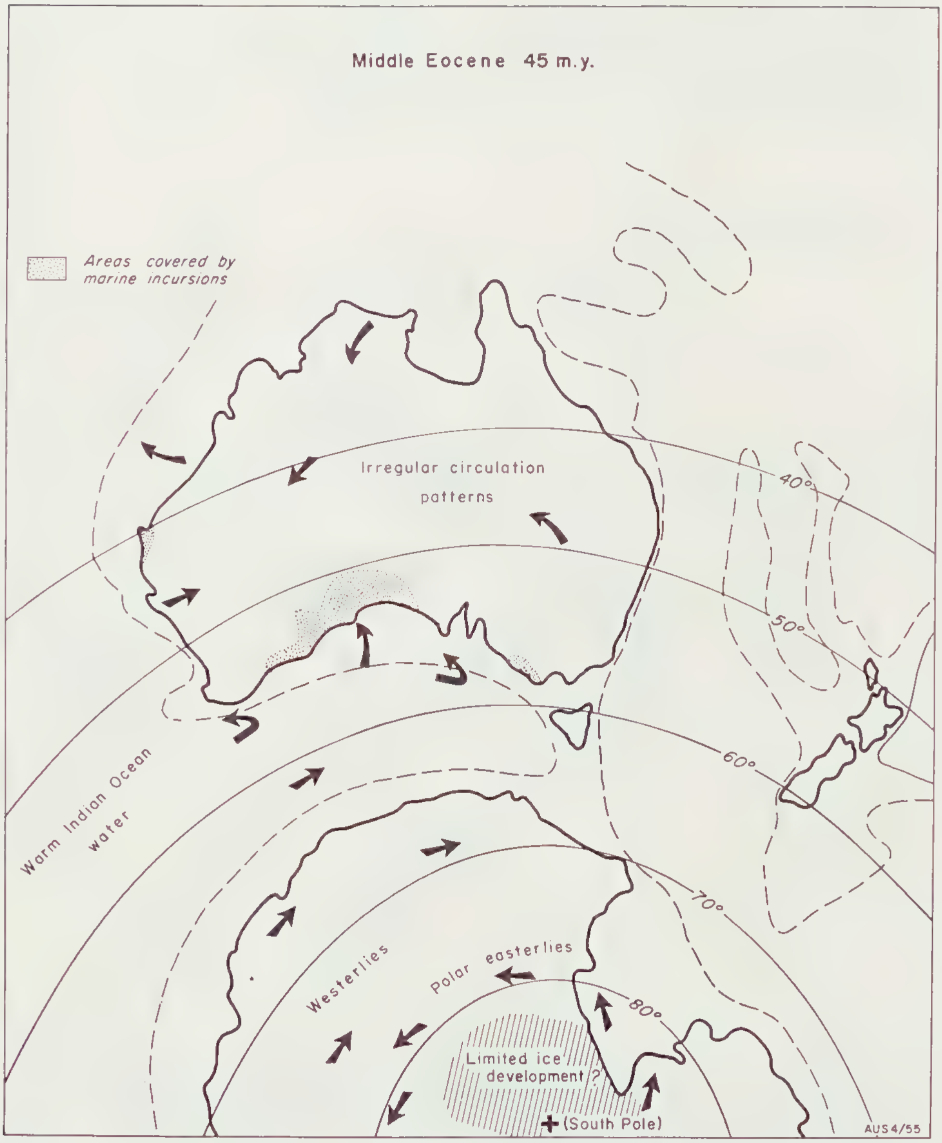


Figure 10. Palaeogeographical reconstruction of the Australian region for the middle Eocene (45 m.y. BP), with tentative atmospheric palaeocirculation shown by heavy arrows. Transgressive seas shown in stipple. (From Kemp, 1978; reprinted by permission from *Palaeogeography, Palaeoclimatology, Palaeoecology,* 24: 184)

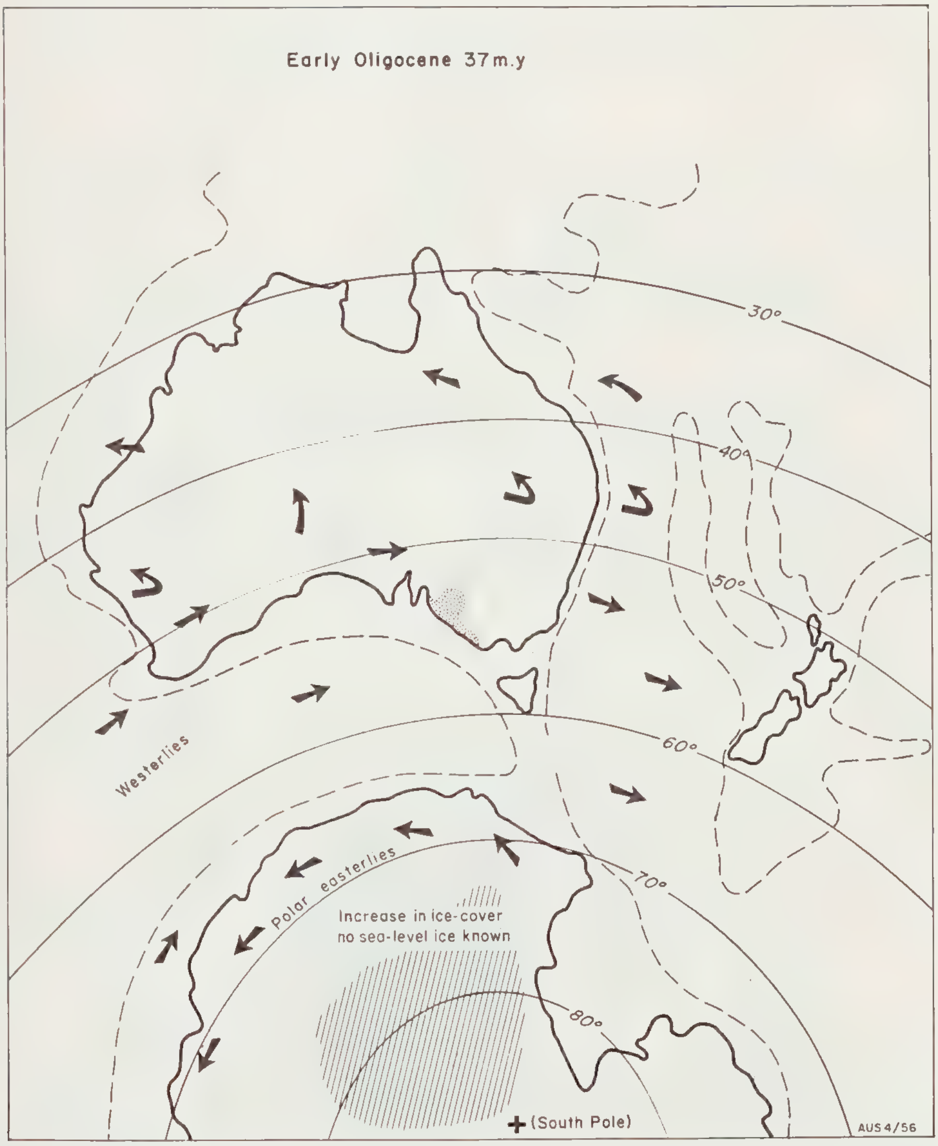


Figure 11. Palaeogeographical reconstruction of the Australian region for the early Oligocene (37 m.y. BP), with tentative atmospheric palaeocirculation shown by heavy arrows. Transgressive seas shown in stipple. (From Kemp, 1978; reprinted by permission from *Palaeogeography, Palaeoclimatology, Palaeoecology,* 24: 192)

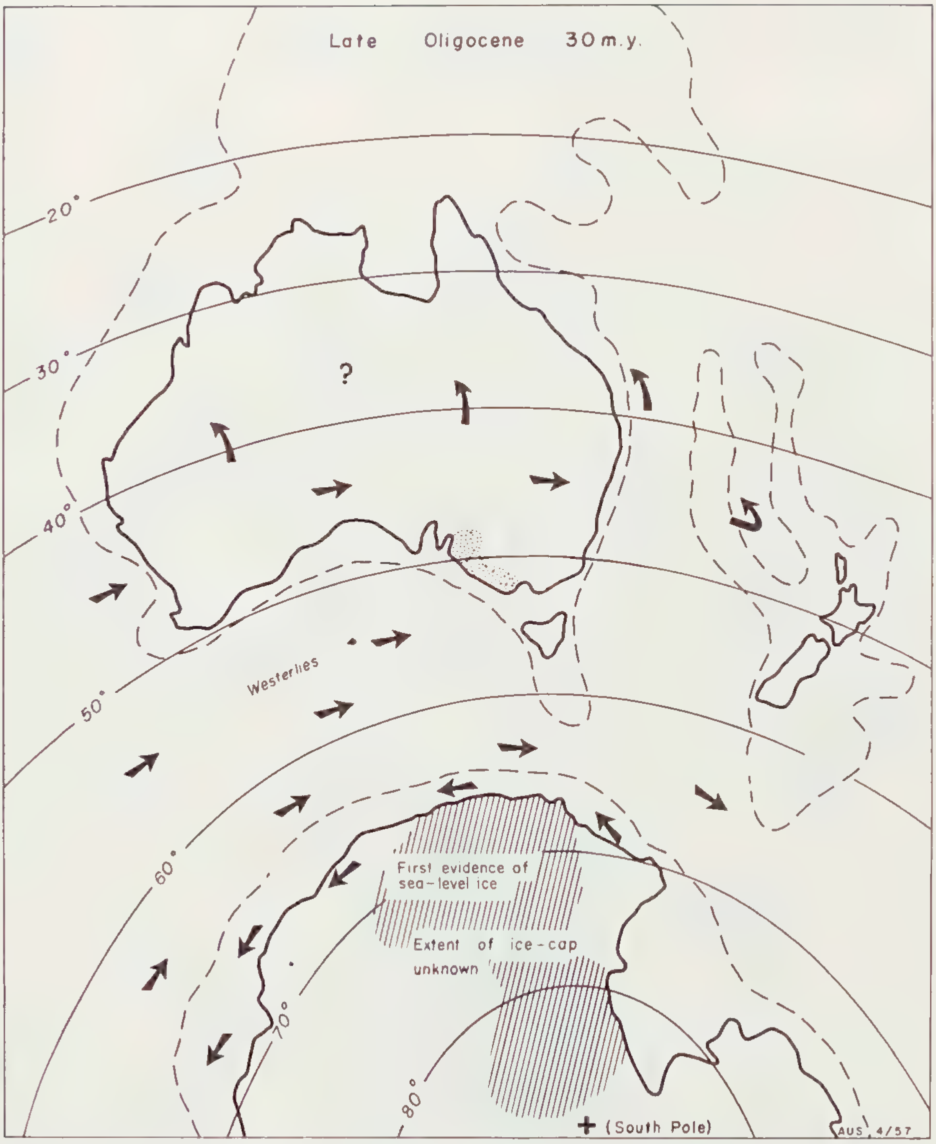


Figure 12. Palaeogeographical reconstruction of the Australian region for the Oligocene (30 m.y. BP), with tentative palaeocirculation patterns shown by heavy arrows. Transgressive seas shown in stipple. (From Kemp, 1978; reprinted by permission from *Palaeogeography, Palaeoclimatology, Palaeoecology,* 24: 193)

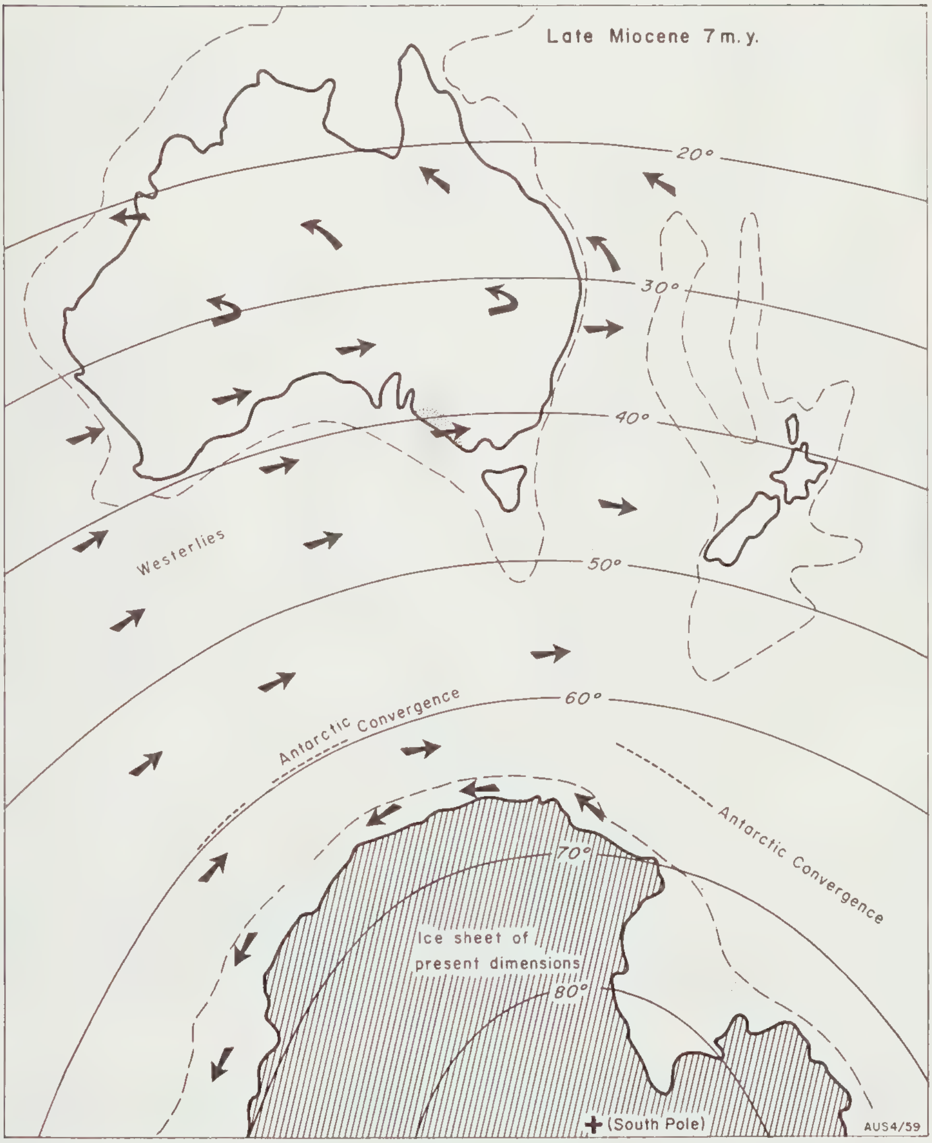


Figure 13. Palaeogeographical reconstruction of the Australian region for the late Miocene (7 m.y. BP), with tentative atmospheric palaeocirculation patterns shown by heavy arrows. Transgressive seas shown in stipple. (From Kemp, 1978; reprinted by permission from *Palaeogeography, Palaeoclimatology, Palaeoecology,* 24: 198)

By late Miocene time the Antarctic ice sheet had reached its present dimensions (Kemp, 1978). Atmospheric circulation increased in intensity, perhaps exceeding that of the present. In parts of Australia levels of precipitation would have fallen and the first onset of a general aridity may have occurred (Kemp, 1978; Bowler, 1981; see below). There is evidence of an ice-surge at the Pliocene boundary, about 5 m.y. BP (Kemp, 1978; Trusswell & Harris, 1981). This would have produced a lowering of temperatures in Australia and an increase in dry anticyclonic circulation. A Pliocene warming followed, then a second cooling in the late Pliocene. These cycles were part of a trend towards cycles of aridity which began in the middle Miocene and have become increasingly frequent up to the present time (Specht, 1981c). Late Cainozoic climates in Australia are discussed in more detail below.

Biological consequences of plate tectonics

The effects which continental displacement have had on plant distributions are obviously related to the dispersibility of the plants. Angiosperm dispersibility naturally covers a wide spectrum, but a surprising number of plant geographers have taken a narrow view of the effective limits of plant dispersibility. For example, the Hawaiian Islands have never been close to continental land and, since their origin, must have been colonised entirely through long-distance dispersal (Carlquist, 1966; Baker, 1967). There is no physical evidence to support the view that land bridges have been involved although a number of workers, including Croizat (1952) and van Steenis (1963), have argued their former existence. At least 272 immigrant ancestral species are required to explain the 2 000 indigenous species in the islands today (Fosberg, 1948).

At the other extreme are families or genera with very limited dispersibility, for which any zone of unfavourable territory represents an absolute migration barrier. They often prove to be strongly continental in their distributions. Groups close to this end of the spectrum include the Proteaceae (Johnson and Briggs, 1975), *Nothofagus* and the southern gymnosperms (Preest, 1963) and the Loranthaceae (Barlow, 1981a). In the latter case the family has not even recolonised Tasmania (see below), and Keast (1958) has shown that although the seeds are bird-dispersed the likely dispersal range is very small. Similarly, species dispersal for this family across Torres Strait has probably been mainly over continuous land (Barlow, 1972).

For many taxa with high dispersibility, the positions of the continents have little effect on distribution, and plate tectonics may be unimportant. Highly dispersible groups are well represented among coastal habitats and a number of cosmopolitan families are common in such habitats. For groups of moderate dispersibility, changes in the proximity of drifting land masses can obviously make or break migration routes. For groups of low dispersibility, migration only over continuous land can be postulated.

These and other consequences of plate tectonics have been well summarised by McKenna (1972). Epicontinental flooding on a world wide scale may have occurred in lowlands due to water displacement at times of spreading maxima, thus causing mass extinction which would have been followed by recolonisation and adaptation at times of reversal. Indeed there was a great spread of epeiric seas in the Australian region associated with the Cretaceous fragmentation of Gondwanaland (Coleman, 1980). The effects of continental rifting would be gradual but quite profound, with the first stage little more than a major extension of coastline (cf. the Red Sea). With widening of the rift, however, continental climates would be moderated and changes in oceanic circulation could lead to general changes in climate. Climatic changes would also be predicted where a drifting block moved through different climatic zones. These processes would obviously result in massive changes in plant habitats and thus in adaptation, extinction and/or migration. Separation of continental blocks would also be a major cause of disjunct distributions and the evolution of vicarious pairs of taxa.

Similarly, collision between continental plates would evoke a gradual rather than an abrupt biological response. Ecologically, marine habitats would be destroyed and new upland or alpine habitats created, again leading to extinctions and adaptation and colonisation respectively. Floristically, exchange between the approaching floras would commence with colonisation by the more highly dispersible taxa while the blocks were still well apart. Competition and adaptation would thus occur progressively even before contact, so that a massive 'invasion' of one biota into the area of another might be unlikely to occur as a single event. Upon actual contact, a filtered migration along a corridor might occur, followed by general exchange across a broad front when contact became extensive, and by colonisation of the new habitats created. Given the time periods involved, competition for niche space could remain high throughout a collision event.

McKenna (1972) also raised the possibility of drifting continental blocks ('Noah's Arks') resulting in a one-way transfer of biota from one area, through rifting, to another area on collision. Again, the collision effects would be gradual, with the Noah's Ark biota probably greatly modified even before collision occurred.

The implications of continental movements for the interpretation of fossil data are obvious, since fossil assemblages can be moved considerable distances from their place of formation. Additional geophysical processes which also make it necessary to consider the location and conditions of deposition include linear transform faulting and latitudinal tilting as a result of polar wandering. Lateral motion along the Alpine Fault in New Zealand, for example, is estimated to be 1 200 km (Griffiths & Varne, 1972).

The new biogeography of Australia

Age and origin of the angiosperms

The flowering plants are usually assumed to be monophyletic, largely because certain basic features such as double fertilisation and triploid endosperm are unique to the group and constant within it. A corollary to this theory is that the angiosperms have radiated from a single place of origin. However several authors have argued that there are several archetypes of the angiosperms and consequently have concluded that they are polyphyletic. For example Krassilov (1977) has suggested that three major Cretaceous angiosperm stocks, viz., Hamamelidales, Laurales and monocotyledons have been derived independently from three Mesozoic 'proangiosperm' seed plant groups respectively, viz., Dirhopalostachyaceae, Caytoniales and Czekanowskiales. Other authors, such as Cronquist (1968), have expressed some uncertainty and have described the various angiosperm features as 'having evolved separately in different lines'.

While the question of the origin of the angiosperms is still unresolved, there is no doubt that they had achieved a wide distribution well before the rifting and separation of the supercontinents. Monosulcate pollen, which is characteristic of the monocotyledons and of the Annonales and Nymphaeales among the dicotyledons, is known from Barremian (Lower Cretaceous) beds in Europe and North and South America (Raven & Axelrod, 1974). Tricolpate pollen, which is characteristic of all other dicotyledons, is also known from beds of similar age at several widespread localities, and an origin in western Gondwanaland has been suggested for this group by Brenner (1976) and strongly supported on several grounds by Raven and Axelrod (1974). By mid-Cretaceous times angiosperms were widespread, their pollen had become more abundant in the record than fern spores and gymnosperm pollen, and a few modern families may have existed. By the end of the Cretaceous, numerous modern families and even genera were definitely present. Thus many present-day groups were present 90 m.y. BP when direct exchange between Africa and South America was still possible. All but the most recently derived families existed when direct migration between South America and Australia via Antarctica was still possible 45 m.y. BP (Raven & Axelrod, 1974). This interpretation bears out the conclusions on southern hemisphere plant distribution reached much earlier by Camp (1947, 1952).

Current evidence suggests that the angiosperms did not originate in Australia but reached the region by migration from other parts of Gondwanaland. The oldest known Australian angiosperm pollen flora significantly post-dates that of northern Gondwanaland and consists of monosulcate types of early Albian age (Dettmann, 1981). Tricolpate forms date from the middle Albian, and the sequential introduction of pollen types is later in Australia than in northern and western Gondwanaland. Dettmann (1981) has concluded that the introduction of angiosperms into Australia was an Albian event, c. 120 m.y. BP, and was perhaps 5 million years later than the inception of angiosperms in northern Gondwanaland and southern Laurasia.

The Gondwanan flora in Australia

The original angiosperm flora of Australia was presumably derived from immigration over broad fronts and probably already showed a wide range of ecological adaptation. Raven and Axelrod (1974) have suggested that a subtropical migration route from Africa to Australia via India may have persisted until middle-late Cretaceous times (Fig. 14), and that until the late Cretaceous there may still have been exchange between Australia and the rifting Madagascar and India. Even after this migration route was broken a south temperate route to Australia from South America via Antarctica remained, perhaps until the Oligocene (Raven, 1979). At this time there were forests of *Nothofagus* and southern gymnosperms, Proteaceae and Myrtaceae to at least 77°S latitude in Antarctica (Kemp & Barrett, 1975; Thomson & Burn, 1977).

A scenario is thus presented for an Australian flora at the beginning of the Tertiary period, with Australia still broadly connected to Antarctica but well separated from Africa, New Zealand and India. Climatic conditions were warm and moist; high rainfall was general in southern Australia and extended through the interior. Temperatures were high in northern and inland Australia (Wopfner et al., 1974) and warm (20–25°C) in southern Australia. The vegetation was more or less uniform structurally, with closed subtropical rainforest being more or less continuous. Some ecological zonation probably existed, with limited differentiation in floristic composition between the warmer and more temperate habitats. This is probably the only sense in which there has been a pan-Australian flora, a concept first proposed by Diels (1906) and later accepted by several authors after it was developed by Crocker and Wood (1947). The pan-Australian flora was Gondwanan rather than autochthonous as visualised by many of these authors. The southern beech *Nothofagus* was already widespread, as were plants referable to *Araucaria*, *Podocarpus*, *Dacrydium*, *Anacolosa* (Olacaceae), Cupanieae, Myrtaceae, *Nipa* and several Proteaceae.

Critical studies of a number of plant groups have further strengthened the argument for an ancient Gondwanan element in the Australian flora. Not unexpectedly, there is a strong Gondwanan character in certain Australian fern groups and in the gymnosperms (Page & Clifford, 1981). Ancient establishment in the Australian flora has also been postulated for the Myrtaceae, Proteaceae and Restionaceae (Johnson & Briggs, 1975, 1981), Loranthaceae (Barlow & Wiens, 1971; Barlow, 1981a), *Rhododendron* and *Vaccinium* (Specht, 1981c), and even for such an advanced and specialised group as the Poaceae (Clifford & Simon, 1981). Raven and Axelrod (1974) have listed many families in 15 orders, the ancestors of which may have reached Australia in Cretaceous times by a subtropical route from Africa. These include, among others, Goodeniaceae, Casuarinaceae, Epacridaceae and Pittosporaceae.

The Tertiary evolutionary history of the Australian flora has thus been one of differentiation from the original Gondwanan stock. The process occurred under conditions of increasing geographical isolation from the time of Australia's separation from Antarctica in the early Tertiary until its contact with the Sunda plate in the Miocene. It was in response to progressive climatic changes until, in the Miocene, conditions were established which were comparable with those of the present. The climatic changes, involving decreasing mean temperatures, increasing intensity of oceanic circulation and of atmospheric circulation, regional decreasing precipitation and increasing seasonality, would have resulted in an increase in the level of habitat differentiation. The earlier pan-Australian flora would have thus undergone differentiation into a spectrum of ecological associations.

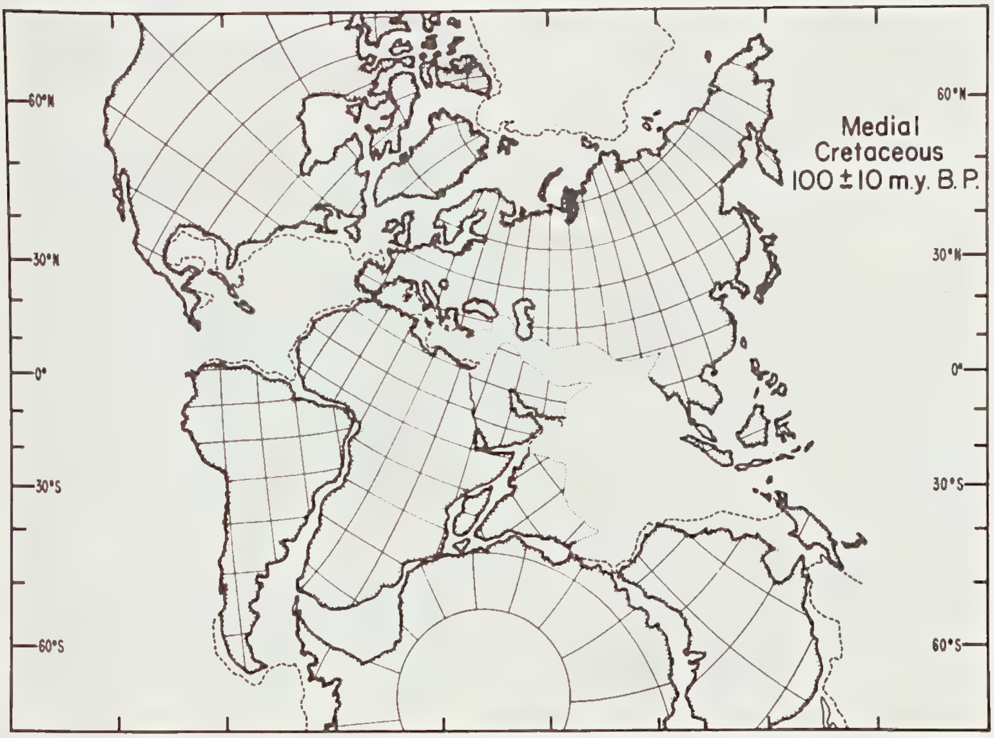


Figure 14. Conformation of the southern continents at the time of establishment of the Gondwanan flora in Australia. (From Raven & Axelrod, 1974; reprinted by permission from *Ann. Missouri Bot. Gard.* 61: 541)

The autochthonous element of the Australian flora thus emerges as the derived one rather than the most ancient one. It simply comprises those components of the flora which have undergone considerable evolutionary change, under conditions of geographical isolation, to produce typically Australian taxa with high levels of endemism. The so-called Indomalayan and Antarctic elements are now seen as comprising, at least in part, the present-day survivors of the Gondwanan flora which have been conservative in the evolutionary sense.

The major floristic composition of the Australian vegetation was thus laid down by the middle of the Tertiary period. It is Gondwanan in origin. It exists today as two components with a relatively strong ecological differentiation. One is the relictual component, consisting of taxa confined to moist habitats (usually closed forests), showing little evolutionary diversification, and showing a residual taxonomic affinity with the floras of similar habitats in the other southern lands. The other is the derived Australian (autochthonous) component, predominantly temperate and arid-adapted, showing massive evolutionary diversification from the more labile of the ancestral Gondwanan stocks and characterised by scleromorphy and high endemism. Nelson (1981) has termed this entire flora the Gondwanic element, and the two components the relict and autochthonous sub-elements respectively.

The flora has been moulded and added to by later geophysical and climatic events. Of major significance has been an apparent geographical isolation of the temperate floras of eastern and western Australia. It may have been initiated by marine incursions into southern Australia which were possibly continuous from late Eocene to mid-Miocene times (Nelson, 1981). The emerged sediments have since remained as dry land and form the limestones of the present Nullarbor Plain. Subsequent increases in aridity (Crocker & Wood, 1947; Raven & Axelrod, 1974) may have maintained an edaphic and climatic barrier between east and west to the present, with little interruption (Nelson, 1981).

The isolation is reflected in the high level of specific endemism in the flora of the south-west of Western Australia, estimated at 87 per cent by Beard (1969) and modified to 68 per cent by Marchant (1973a) and to 75–80 per cent by Hopper (1979). Generic endemism is low and there are many vicarious species pairs in eastern and western Australia. This is consistent with the imposition of isolation at a time when the major genera of the autochthonous sub-element were already widely established.

The extremely species-rich flora of the South West Botanical Province of Western Australia, with its high specific endemism, is attributed to its long history of development in geographical isolation, on a relatively stable land surface on which a mosaic of soil types has evolved. There is little to support the view of some floristic analysts that this richness indicates that the autochthonous flora originated in Western Australia. It has been shown by Hopper (1979) that the greatest species density occurs in the transitional rainfall zone between the mesic forest areas and the arid zone, and that a high proportion of the species are very local endemics within this zone. He concluded that in the more recent geological past conditions have been more favourable for speciation in this zone than in the more mesic and more arid zones. In particular, he has pointed out that recurrent climatic fluctuations would have generated greater stresses in the transitional zone and, coupled with the evolution of a mosaic of nutrient-deficient soils, would have produced disruptions in labile population systems ideal for rapid speciation.

The corollary to species richness is that many species have very small geographical ranges because of their geographical replacement patterns. This is true of *Adenanthos*, *Stylidium*, *Darwinia*, *Eucalyptus*, *Banksia* and *Acacia* (Nelson, 1981). In *Stylidium*, cross-compatibility between neighbouring populations of a species is often low (Farrell & James, 1979), indicating that selection for reproductive isolation between neighbouring populations is very high. This phenomenon may be associated with the maintenance of highly adaptive local biotypes under conditions of intense competition on nutrient-deficient soils.

As mentioned above, the karyoevolutionary data of Smith-White and others can be reconciled easily with the current view of the history of the Gondwanan element. Their studies revealed recurring patterns of chromosome number variation in which autochthonous groups showed greater diversity than non-endemic or extra-Australian ones, with polploidy apparently superimposed as a tertiary phase on extensive secondary dysploidy. In addition to the several groups cited above, subsequent studies have revealed comparable patterns in a number of other groups, including Restionaceae (Briggs, 1963), Papilionaceae (=Fabaceae) (Sands, 1975), Stackhousiaceae (Turner, 1966), Droseraceae (Marchant, 1973b), *Stylidium* (James, 1979) and *Hibbertia* (Stebbins & Hoogland, 1976). The dysploid changes can now be seen as devices which have conserved adaptive biotypes during the differentiation of the autochthonous sub-element; they have served to restrict gene pools, thus favouring diversification, but have led to a new stability in the derived groups. This explains why dysploidy is so characteristic of the generic rank or its equivalent. Further genetic conservation of adaptive biotypes has very frequently involved polyploidy, both in woody and herbaceous groups. As pointed out by James (1981), these changes illustrate the 'unceasing selection of conservative devices which ensure minimal departures from already tested adapted parental genotypes'. It is noteworthy that within this framework of genetic conservation a number of groups have evolved mechanisms which maximise genetic heterozygosity.

The parallel karyological patterns thus illustrate the condition under which the autochthonous sub-element has evolved—strong selection, under conditions of strong competition, for the maintenance of highly adaptive new biotypes as they have arisen under progressively changing environmental conditions. This pattern has been developed most strongly in the scleromorphic flora of nutrient-deficient soils, particularly under developing temperate conditions.

An expression of uniqueness—scleromorphy

The most striking aspect of the autochthonous element is its scleromorphy. Many of its major groups are characterised by relatively small, rigid leaves, by short internodes and by small plant size. There is a strong representation of such types in Australian Myrtaceae, Proteaceae, Rutaceae, Epacridaceae, Mimosaceae, Fabaceae and Goodeniaceae. It was generally assumed by earlier botanists that scleromorphy in the Australian flora represented adaptive responses to an increase in aridity, and in particular to the advent of mediterranean climate. An exception was Andrews (1916), who linked scleromorphy with soil properties and suggested that it was an adaptive response to low levels of soil nitrogen and calcium. More recently several authors have taken up the idea that scleromorphy is an adaptive response to nutrient deficiency (Beadle, 1954, 1966, 1968, 1981; Johnson & Briggs, 1975, 1981; Loveless, 1961; Specht, 1972). Its expression is accepted as a response to chemical constraints on growth and as a physiological process marked, among other things, by a reduction in the number of cells formed. Beadle (1954, 1968) suggested that soil phosphorus levels regulate soil nitrogen fixation and that phosphorus status is the basis of scleromorphy as a physiological adaptation.

Conditions favouring the evolution of scleromorphy in the Australian flora probably existed early in the Tertiary period. Specht (1981b) has pointed out that heath communities are part of the moist tropical ecosystem, forming a mosaic with closed forest communities and occurring on deep infertile sandy soils. They share families and genera in common with rainforest. Beadle (1981) has suggested that scleromorphy began to differentiate at the margins of rainforest, proceeding along declining soil fertility gradients. This view was shared by Johnson and Briggs (1981), who discussed the evolution of scleromorphy in relation to their analysis of relationships in the Myrtaceae, Proteaceae and Restionaceae. They argued that the differentiation of scleromorphic taxa began at least in early Tertiary times in nutrient-deficient forest sites, possibly catalysed by climatic change, and that the process has continued through successive differentiations as the climate has been progressively modified. Because so much of the Australian land surface has undergone weathering continuously for a long time, poor soils are now the rule. Conditions favouring scleromorphic vegetation in Australia have therefore become progressively more widespread, resulting in an expression of scleromorphy not matched in other continental floras.

Scleromorphy may have been a pre-adaptation to mediterranean climate, so that the scleromorphic flora may have colonised the habitats where this climatic regime was established later in the Tertiary. The scleromorphic flora has, however, remained confined to low-nutrient soils even under increasingly dry conditions, not effectively spreading onto adjacent high-nutrient soils. Van Steenis (1979) has pointed out that this feature of scleromorphic communities may explain the very limited representation of an Australian floristic element in Malesia (see below).

The post-Miocene intrusive element

Another major event in the history of the Australian flora was its late-Tertiary contact with that of the Indomalayan region. The Miocene collision between the Australian plate and the Sunda arc brought together two rich floras which, until then, had been isolated from substantial direct exchange for a considerable period. The geological history of the north-western margin of the Australian plate has been very complex, however, and the way in which these two floras came in contact is not clear. It was suggested by Audley-Charles et al. (1972) that Timor and several other islands of the Outer Banda Arc, and even the eastern part of Sulawesi (Celebes), formed part of the north-western margin of the Australian plate through the Mesozoic and much of the Cainozoic. A more general view, however, is that Timor formed part of the margin of the Australian plate and that the other islands were part of the Outer Sunda Arc (Grady & Berry, 1977; Powell et al., 1981). Timor may therefore represent a limited exception to the suggestion by Raven (1979) that no part of Indonesia was ever part of Gondwanaland. Southern New Guinea also formed part of the Australian plate margin to the north (Fig. 15).

In Miocene time the leading edge of the Australian plate collided with the Sunda Arcs, first involving the New Guinea margin of the plate, and later the margin further west (Powell et al., 1981). At this time the Sundaland plate was moving westwards, and as the Australian plate continued northwards the Sunda Arcs were contorted into the great fold which now accounts for the position of islands such as Sulawesi and Seram, north of the Inner Arc islands such as Sumbawa. These islands have probably increased to their present size as a result of the collision effects. With the continued westward rotation of the Sundaland plate since the collision occurred, the distance between Australia and these lands has subsequently increased again. The chronology of these events was interpreted similarly by Audley-Charles et al. (1972), but their interpretation differs in that they postulated the collision and rotation of the Outer and Inner Sunda Arcs as the margins of the Australian and Sundaland plates respectively (Figs 15–17).

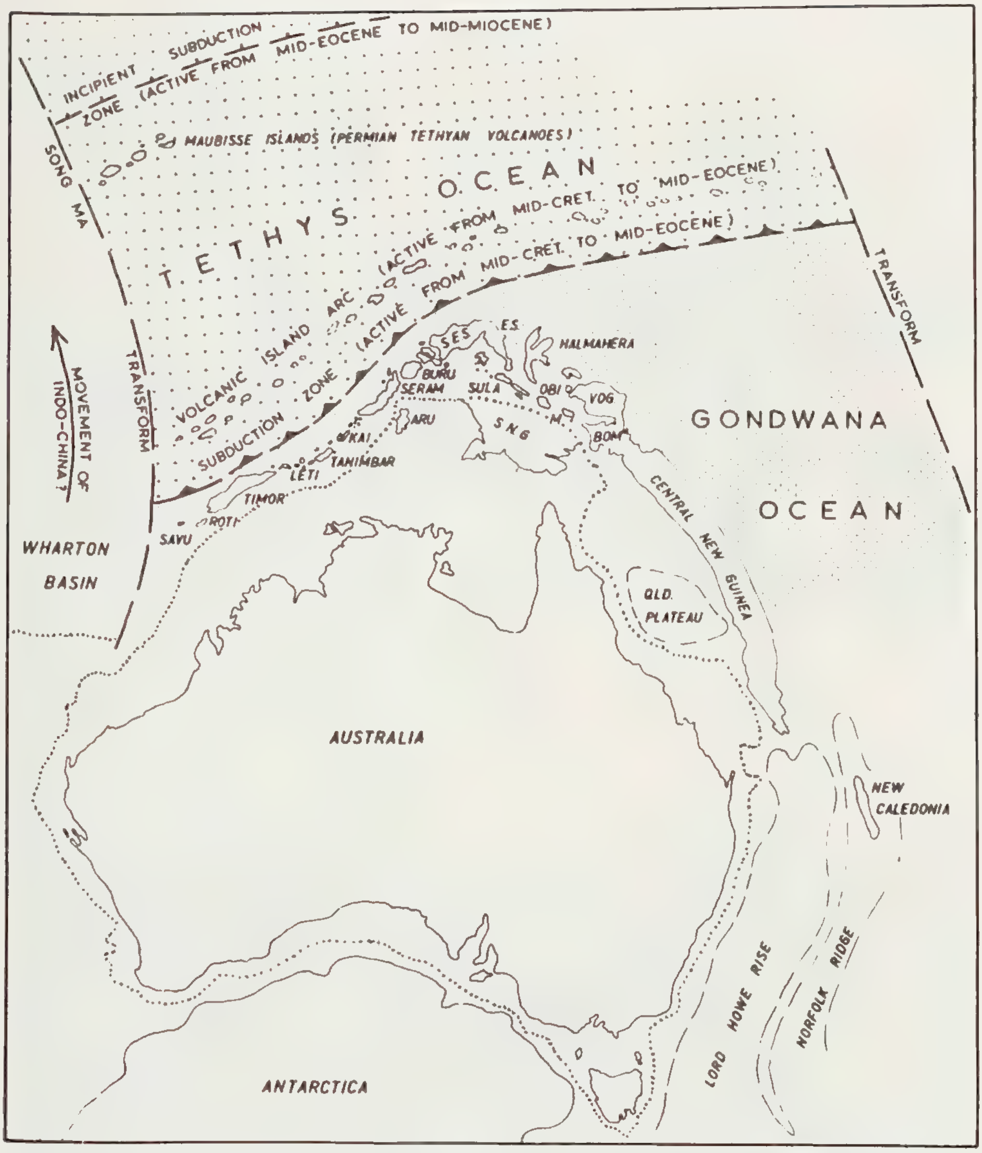


Figure 15. Reconstruction of part of Gondwanaland showing the position of New Guinea and eastern Indonesia during the late Cretaceous. The present-day outlines are shown for reference and have no palaeogeographical significance. The proposed position of the volcanic island arc is related to the northward drift of Australia-Antarctica initiated in the mid-Cretaceous. BOM = Bomberai; VOG = Vogelkop; M = Misool; E.S. = East Arm and S.E.S. = South-east Arm of Eastern Sulawesi; S.N.G. = South New Guinea province. (From Audley-Charles et al., 1972; reprinted by permission from *Nature Phys. Sci.* 239: 35–39. © 1972 Macmillan Journals Ltd.)

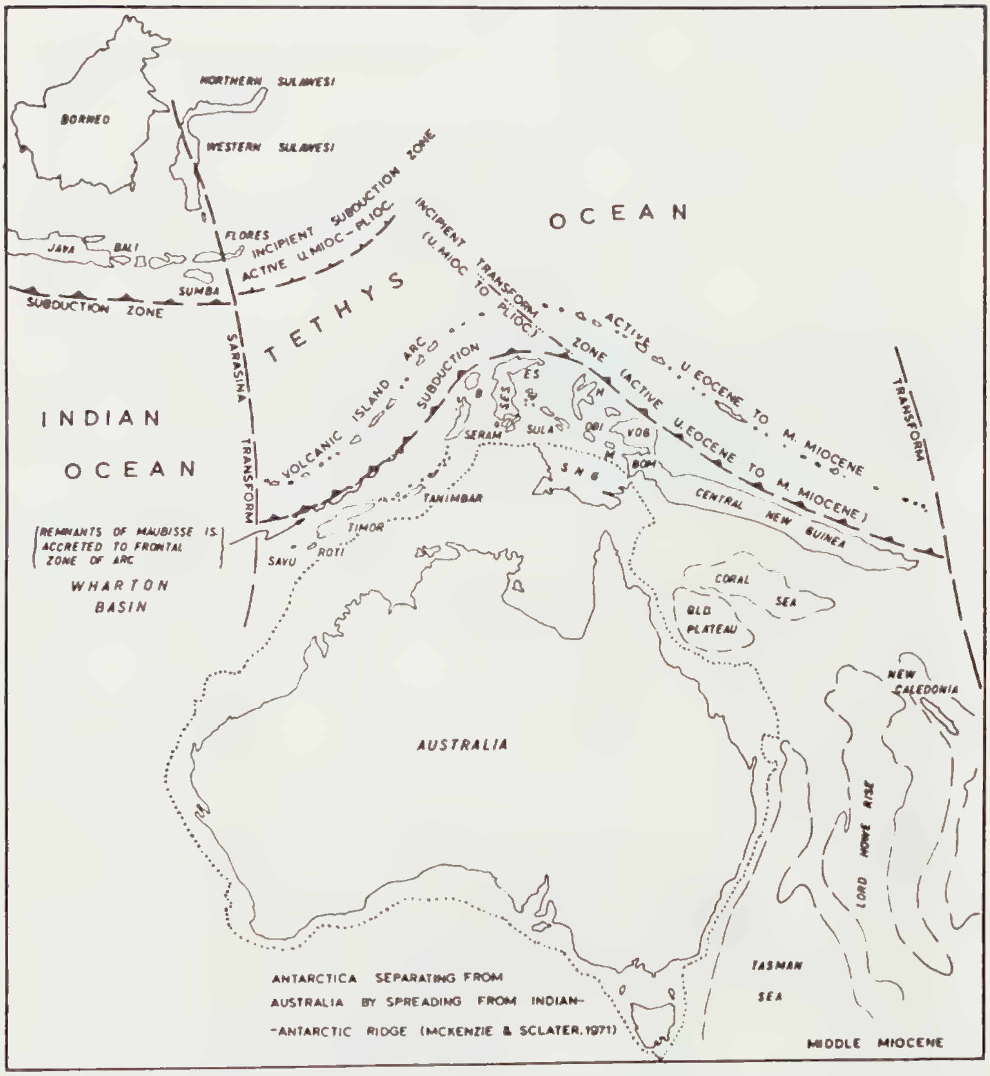


Figure 16. Reconstruction of Australia showing its relationship with Indonesia and part of Melanesia during the Middle Miocene. The present-day outlines are shown for reference and have no palaeogeographical significance. Note the opening of the Coral and Tasman Sea basins and the anticlockwise rotation of Central New Guinea, eastern Sulawesi, Buru and Seram. Northward-drifting Australia had separated from Antarctica. B = Buru; H = Halmahera; M = Misool; BOM = Bomberai; S.N.G. = South New Guinea province; S.E.S. = South-east Arm and E.S. = East Arm of eastern Sulawesi. (From Audley-Charles et al., 1972; reprinted by permission from *Nature Phys. Sci.* 239: 35–39. © 1972 Macmillan Journals Ltd.)

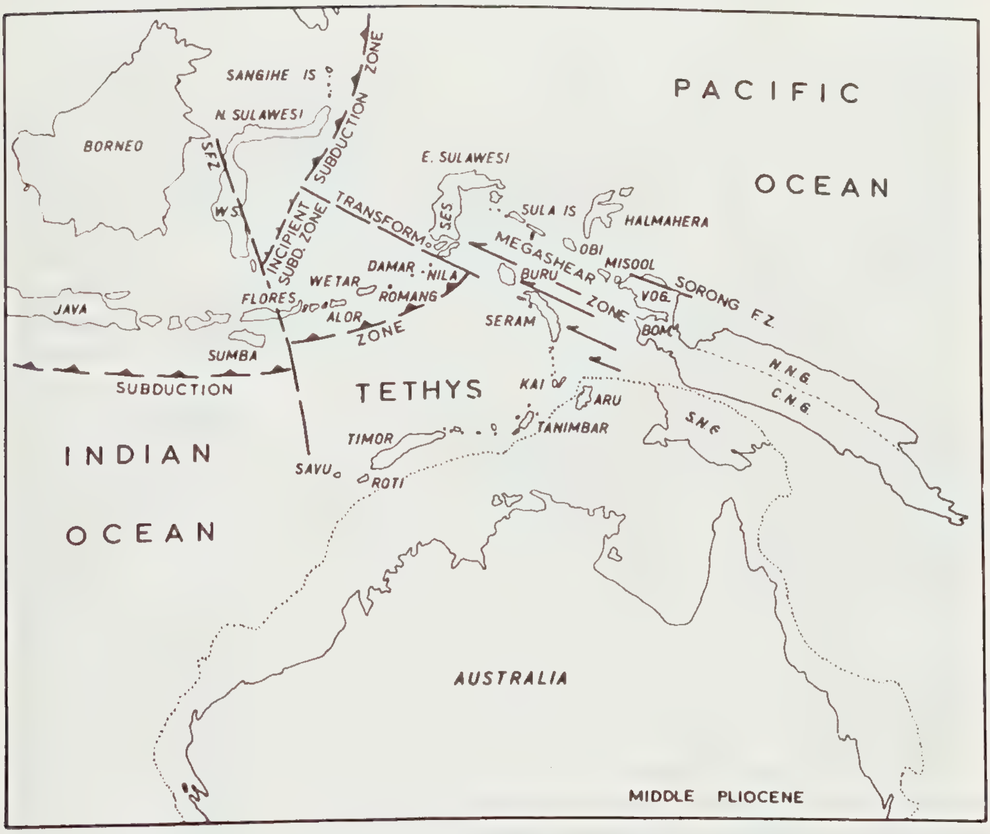


Figure 17. Reconstruction of northern Australian margin, New Guinea and eastern Indonesia during the middle Pliocene. Note progressive development of the island arc systems related to the northward drift of Australia. The present-day outlines are shown for reference and have no palaeogeographical significance. BOM = Bomberai; VOG = Vogelkop; N.N.G. = North New Guinea province; C.N.G. = Central New Guinea province; S.N.G. = South New Guinea province; S.E.S. = South-east Arm of eastern Sulawesi; W.S. = Western Sulawesi; S.F.Z. = Sarasina fault zone; Sorong F.Z. = Sorong fault zone. (From Audley-Charles et al., 1972; reprinted by permission from *Nature Phys. Sci.* 239: 35–39. © 1972 Macmillan Journals Ltd.)

There are various interpretations of the formation of the present island of New Guinea. Audley-Charles et al. (1972) postulated a rotational movement which brought component blocks together on the northern margin of the Australian plate (Figs 16, 17). Simpler explanations involve northern New Guinea being an island arc beached and uplifted against southern New Guinea as the Australian plate moved north (Raven, 1979), or northern and southern New Guinea having been continuously in close proximity and eventually united by the uplift of a trough between them (Crook, 1981).

The present Indonesian Archipelago and the Papuasian region are therefore derived from a complex interaction between parts of the Australian plate and the Pacific and Sunda arc systems. Floristic exchanges as a result of this contact have occurred in both directions, resulting in a limited integration of the Gondwanan and Laurasian floras in the Malesian and western Pacific regions. Because such a diversity of primitive relictual angiosperms occurs in the area today, some authors have suggested it as the site of origin of the angiosperms (Takhtajan, 1969; van Steenis, 1971). The turbulent geological history of the area, and our present knowledge of the sources of its flora, make this idea clearly untenable (Schuster, 1976).

The so-called Australian element in the Sundaland region is highlighted by a few species in genera such as *Casuarina*, *Araucaria*, *Banksia*, *Grevillea*, *Acacia* and *Eucalyptus* (van Steenis, 1936). This element has been over-emphasised because of the distinctive nature of the species involved (van Steenis, 1950) and by the erroneous inclusion of genera such as *Casuarina* which have had a much longer history in the region. Nevertheless a number of Australian taxa have penetrated into Sundaland, including *Ptilotus* (Stewart & Barlow, 1976a), *Stylidium* (Erickson, 1958) and several grasses (Clifford & Simon, 1981). Van Steenis (1979) has listed 98 'eastern or south-eastern' species, with a variety of lifeforms, in the flora of the Lesser Sunda Islands, and of these 65 also occur in Australia, many of them in genera which are well developed in Australia. In the Loranthaceae the *Amyema* group of genera, with $x=9$ and large chromosomes, is Papuasian in origin but has spread and diversified in the Philippine and Sunda regions.

Few of the Australian taxa which have penetrated Sundaland have extended beyond it into south-east Asia or beyond (Specht, 1981c), presumably owing to the richness and stability of the Laurasian flora, and to the general lack of nutrient-deficient soils, to which much of the Australian flora is adapted (van Steenis, 1979). A few Australian grass genera have reached south-east Asia (Clifford & Simon, 1981). In *Dodonaea*, which has apparently had a long history in tropical and temperate Australia, one pioneering species complex has dispersed widely through south-east Asia and Africa, as well as to the New World (West, 1980); its lack of diversification indicates that this range extension is relatively recent.

Migration in the reverse direction has been more significant. New Guinea has been colonised predominantly from the Malaysian region following its elevation above sea level at the end of the Oligocene (Raven & Axelrod, 1972). Secondary exchanges from New Guinea, and direct immigration from Sundaland, have contributed a significant component of the Australian flora, especially in tropical ecosystems. This is reflected in the low frequency of endemic genera in Australia's tropical zone (14 per cent, Burbidge, 1960), compared with that of the temperate zone (46.6 per cent). Burbidge (1960) noted that a high proportion of the non-endemic Indomalayan genera in the tropical zone have only one or few species in Australia. This can be explained as a result of relatively recent immigration into a floristically rich region in which diversification has been restricted by stabilising selection. Burbidge's analysis showed that in the tropical zone there are 360 non-endemic genera represented by a single species in Australia and 320 genera represented by 2–5 species. It should be borne in mind, however, that the same data could support the existence of a Gondwanan component in the tropical flora, and the significance of such a component in the tropical flora should not be overlooked when Burbidge's data are considered.

In Loranthaceae, two groups of genera appear to have entered the Australian-Papuasion region as a result of the contact with the Indomalayan flora. The *Decaisnina* group of genera, with $x=12$ and large chromosomes, is an excellent example of an Indomalayan stock in which one or a few species of several genera have reached the region (Barlow, 1981a). Only one genus, *Lysiana*, has originated in the Australian region and undergone a limited radiation into the temperate and arid zones. *Dendrophthoe*, with $x=9$ and small chromosomes, is centred in South-east Asia and is represented by one widespread species extending from India to south-eastern Australia and by a few young endemics in New Guinea and northern and eastern Australia.

The late Tertiary elevation of mountain systems between Malaya and New Guinea has probably provided a dispersal route for cool temperate plants, and this dispersal route may have extended through eastern Australia. Long-distance dispersal between isolated highland regions has almost certainly been involved, as the Indomalayan lowlands have possibly remained continuously warm and humid (van Steenis, 1934a,b, 1936). A number of typically north-temperate genera may have been dispersed to the Australian region by this route and some have apparently undergone new radiations, especially in the New Guinean highlands (Raven & Axelrod, 1972). Genera in Australia which may have had this history include *Veronica*, *Euphrasia*, *Poa*, *Stellaria*, *Ranunculus*, *Ajuga*, *Viola* and some Apiaceae (Burbidge, 1960; Raven & Axelrod, 1972).

Because of the complex floristic history of the southern Asian region, the late Tertiary immigrant flora in Australia may have had diverse origins. In particular, the role of the Gondwanan flora of India may be relevant. The Indian plate rafted from Gondwanaland about 125 m.y. BP and collided with Asia in the middle Eocene, at least 50 m.y. BP (Raven & Axelrod, 1974; Powell et al., 1981). The crustal shortening and elevation of the Himalayas followed later, reaching a peak at the end of the Tertiary period although India is still moving northwards at 5 cm per year. Specht (1958, 1981c) has drawn attention to the strong relationship between the floras of sandstone habitats in monsoonal India and northern Australia, and suggested that these are vicarious remnants of the Gondwanan flora. Other floristic alliances, however, were eliminated as India moved through a succession of climatic regimes on its northward drift (Schuster, 1976). These could have included tropical and temperate southern stocks (Raven & Axelrod, 1974) and heathland flora (Specht, 1981c). India thus carried a reduced flora when it reached Asia, but some of its taxa have spread more widely in Asia (Raven & Axelrod, 1974; Specht, 1981c). Subsequently, with the opening of a direct migration route to Australia, some derivatives of this ancient Gondwanan stock may have re-entered Australia.

The Loranthaceae again provide a likely example of this sequence. While the family is undoubtedly Gondwanan, two generic alliances appear to have had a long history in Asia and one of them secondarily in Africa. These are the *Decaisnina* group of genera and the *Dendrophthoe* group, described above. It seems plausible that the ancestors of both groups reached Laurasia via India in early Tertiary times and underwent extensive secondary radiations there. The former group now comprises more than 100 species in South-east Asia and Indomalaya, while the latter is represented by about 100 species in Asia, the Middle East and southern Europe and by the entire loranthacean flora of Africa (about 300 spp.). As mentioned above, both of these generic alliances have attained a limited representation in Australia as re-colonisers since the Miocene.

The floristic implications for Australia of these events have been well summarised by Nelson (1981). In addition to the Gondwanic element defined above, he has also defined an 'Intrusive element' comprising plants which have entered Australia subsequent to its separation from Gondwanaland. Within this element he has recognised three sub-elements, namely (1) a tropical sub-element consisting of taxa of recent derivation from tropical South-east Asia, (2) a cosmopolitan sub-element of widely distributed genera and species, widespread in Australia especially in arid areas, and (3) a neoaustral sub-element of mainly temperate species derived by recent migration from the northern hemisphere. If the first of these sub-elements is to be viewed as strictly Laurasian, then perhaps we could add (4) an Indogondwanan sub-element, consisting of plants of ancient Gondwanan derivation which have reached Australia as part of the Intrusive element.

The integration of the Australian flora

The Australian flora thus emerges as an amalgum of taxa with diverse histories and potentials. It includes taxa the ancestors of which have been in Australia since the dawn of the age of flowering plants, and it includes a variety of recent colonisers, which in some cases have just established a foothold in Australia and in other cases have diversified at the expense of previous inhabitants. It includes taxa which are evolutionarily conservative, so that their relationships and origins are clearly evident, and it includes taxa which are evolutionarily labile, having diversified and adapted to occupy the spectrum of niches which have arisen through time. The changes which have occurred in the latter group have yielded a distinctive array of genera that are endemic to the region and unique in many aspects of their structure and function. From an integration of palaeobotanical, palaeoclimatic and geophysical evidence, the historical relationships of these components of the flora have now become clear.

While each of the elements and sub-elements of the flora tends to dominate in a particular ecological situation, there is nevertheless a significant integration of these floristic units within each major plant formation in Australia. Specht (1981a,b) distinguished 32 plant formations in Australia, and analysed the distributions of 1 285 genera represented in them. He concluded that almost every one of these formations contains a mixture of genera which belong to different floristic groups in terms of geographical distribution and relationships. That is, the modern Australian flora is differentiated into major plant formations which nearly always include representatives of several of the historical elements and sub-elements of the flora.

The integration of the floristic elements and sub-elements in the flora is illustrated by their growth and flowering rhythms. The flora can be divided into three broad thermal response groups (Nix, 1981; Specht, 1981b), based on the temperatures at which seasonal shoot growth is initiated. These growth rhythms correlate reasonably well with the accepted components of the flora, indicating that they have been retained through a considerable time and climatic sequence. The potential growing seasons of the three groups are within the temperature ranges of (1) > 25°C, (2) 15–25°C, and (3) 10–15°C respectively. Particular plant associations may include more than one of these thermal groups and some members of an association may thus be out of phase with the current climate of the region. Increasing seasonality of the climate has probably had a major role in the fluctuating interactions of these functional components of the flora, perhaps outweighing the effects of aridity *per se* (Nix, 1981).

Three thermal response groups in the herbaceous flora can also be distinguished in another way (Specht, 1981a,b). These are temperate C_3 plants, tropical C_3 plants and tropical C_4 plants, each with a distinctive response of biomass increment to mean daily temperature. Grasses with the C_4 dicarboxylic acid metabolism are perhaps more efficient photosynthetically than C_3 plants and are widespread in most open plant communities in Australia. Among the chenopods, C_4 species of genera such as *Atriplex* and *Maireana* are likewise dominant in arid situations (Parr-Smith, 1981; Specht, 1981b). The C_4 understorey plants have thus had an important role in the differentiation of plant communities in Australia. It is only in closed forests, wet freshwater swamps and montane habitats that C_4 herbs are replaced by those of the C_3 groups. In southern Australia, however, the native C_4 grasses, with a high, out-of-phase temperature threshold for shoot growth, are being replaced by introduced temperate C_3 grasses which are phenologically better adapted, attaining maximum shoot growth at lower temperatures much earlier in the spring.

The climatic events of the more recent past which have influenced the development of the Australian flora after its general character was established have been well documented. An excellent review by Galloway and Kemp (1981) summarises the effects of continental displacement, volcanism, temperature and sea level fluctuations, and their expression in terms of dune formation, vegetation shifts and speciation. Some aspects of this phase of vegetation history are discussed below in relation to the evolution of an arid zone flora, but there are some important general considerations which arise from the data.

In the Quaternary, climatic changes were generally more rapid and extreme than were general in the Tertiary and they have certainly affected Australian biogeography profoundly. This period represents only a small fraction of the time interval in which the Australian flora has developed, however, and the fluctuations appear to have been within the ecological tolerances already well established in the flora. Major vegetational changes indicated by pollen analysis may have been only local migrations of adjoining vegetation types. The record indicates, for example, that tropical rainforest returned to north-east Queensland only about 10 000 years ago after an absence of 70 000 years (Galloway & Kemp, 1981), but it may have been present not far away from the sites examined. Even today there are very steep environmental gradients in the region, with different vegetation types occurring only short distances apart.

This situation has probably existed at least since the early Pliocene. Pollen records suggest a transition from older rainforests, dominated by *Nothofagus* and southern gymnosperms, to open forest dominated by *Eucalyptus*, *Casuarina*, grasses and composites. Nonetheless records of wet forest plants at some sites throughout the epoch again suggest that the vegetation was a shifting mosaic of communities similar to those of the present.

A similar explanation for the history of alpine plants in Australia may be necessary. High mountains have been continuously absent through the Cainozoic (Galloway & Kemp, 1981) and alpine habitats have probably always been limited. They may have been repeatedly eliminated during thermal maxima, and alpine plants may have survived in refugial habitats such as stream banks. The rather disharmonic alpine flora may represent only the surviving remnants of earlier alpine communities.

Torres Strait and Bass Strait — land bridges of the recent past?

New Guinea — a floristic crossroads

A broad spectrum of views on the relationship of the Australian flora with that of New Guinea has been expressed, but there has been a progressive change of view as the palaeogeography and palaeoclimate of the Torres Strait region have become better understood. Van Steenis (1950) argued that Torres Strait was one of the principal floristic 'demarcation knots' of the Old World Tropics. He defined a demarcation knot in terms of the total number of genera which reached their distribution limits in the area concerned. For Torres Strait the demarcation knot was 984, comprising 644 Malesian and endemic genera in New Guinea which were absent from Australia and 340 Australian genera absent from New Guinea. Van Steenis used this concept to argue that New Guinea was part of the Malesian floristic region. The sharpness of the floristic transition across Torres Strait was also emphasised by Good (1960) who stated that of 1 350 indigenous genera in New Guinea, only 62 are Australian (in the sense that the bulk of the species are found in Australia).

While the predominant view of the time was that the New Guinean and Australian floras are quite distinct, not all authors viewed Torres Strait as the boundary between the two. Because of the physiognomic and floristic resemblance of the open savannahs of western Papua and Cape York Peninsula, several authors treated south-western Papua as part of the Australian floristic region (Good, 1963). On the other hand Herbert (1935, 1960) suggested that the rainforest of north-eastern Australia should be included in the Malesian floristic region.

On the basis of current views of late Tertiary and Quaternary palaeogeography the Torres Strait region is now seen as more of an ecological boundary than a geographical one. Following the regression of the sea in the early Tertiary, the northern margin of the Australian plate (including southern New Guinea) remained as dry land (Doutch, 1972). Thus when New Guinea began to assume its present form and relationship with Australia, there was no seaway between the two regions, and by Pliocene times most of New Guinea had emerged and formed the northern part of the Australian land mass. The seaway formed by the Arafura Sea and Torres Strait probably only came into existence in the Pleistocene and it has almost certainly been re-established as a land link at least seven times through subsequent sea level fluctuations (Doutch, 1972; Galloway & Loffler, 1972; Galloway & Kemp, 1981). Torres Strait was most recently formed between 6 500 and 8 000 years ago, and except for a few channels is presently less than 10 metres deep (Jennings, 1972).

The relationship between the Australian and New Guinean floras must therefore be determined on the basis of climatic history. During the last glacial maximum the exposed Torres land bridge and the north of Australia would have been at least as arid as the Carpentaria region is today (Webster & Streten, 1972). Nix and Kalma (1972) have extrapolated from palaeoclimatic data to vegetation types through Quaternary time and have described a pattern of north-south shifts in arid and open woodland vegetation (Figs 18–21). They have pointed out that even if the hypothesis for their calculations is incorrect, there is no doubt that a core area of closed rainforest has persisted in New Guinea and a core area of arid and semi-arid land has remained in Australia.

Torres Strait may thus represent not so much a physical barrier to plant migration as a zone of strong ecological differentiation between the regions on either side of it. Most of the species which occur on both sides of the Strait grow in coastal lowlands and have presumably had access to suitable habitats for migration (Hoogland, 1972). On the other hand there are very few rainforest species common to both sides of the

Strait; sclerophyllous species occupy an intermediate position (Webb & Tracy, 1972). This situation is consistent with the time periods during which their respective habitats have been isolated from exchange. In the main, then, the differences between the Australian and New Guinean floras are probably the result of the long climatic sifting of a single ancestral stock (Wace, 1972). Superimposed on this is the floristic effect of the Indomalayan element (i.e. the tropical sub-element of the Intrusive element in the Australian flora), which has become a major component of the New Guinean flora but which for purely climatic and edaphic reasons has not achieved the same dominance in the flora of northern Australia.

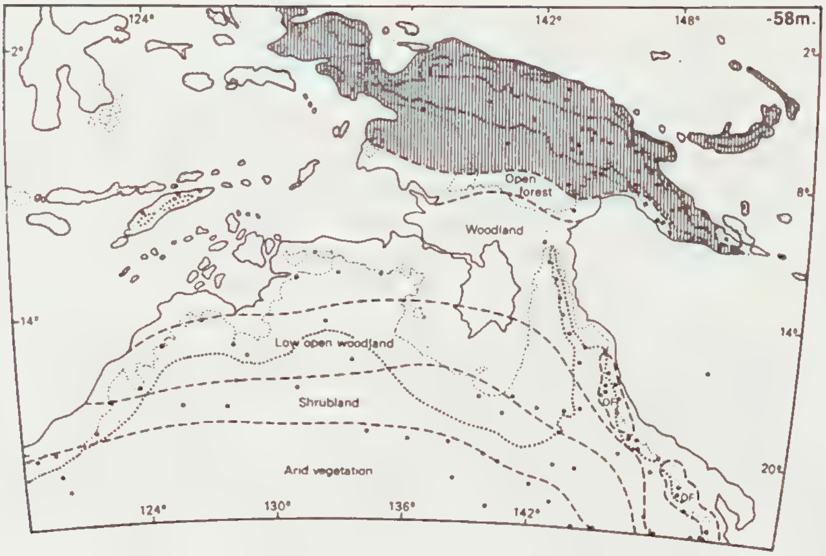
Tasmania — a living piece of Gondwana

The floristic history of Tasmania has been integrally bound with that of the rest of Australia. Tasmania was still part of the Australian mainland at least until the Oligocene or Miocene, when Bass Strait was first formed (Gill, 1962; Galloway & Kemp, 1981). The later Tertiary history is uncertain but it has been the rule, rather than the exception, for Tasmania, mainland Australia and New Guinea to form one land mass during the last million years. Bass Strait has been opened as a seaway at least eight times, the most recent being 13 500–12 000 years BP (Galloway & Kemp, 1981). The common floristic history is reflected by the analysis made by Burbidge (1960), which showed that there are no families of seed plants endemic in Tasmania. About 100 families occur in Tasmania out of about 215 in the whole of Australia. Only 28 of approximately 400 genera (7 per cent) and about 246 of 1 200 species (20 per cent) are endemic. There is therefore a high level of similarity, even at the present day, between the floras of Tasmania and the south-eastern mainland.

Because of its geographical position, its insularity and its relatively mountainous topography, Tasmania has continuously retained an environment similar to that which was widespread in Australia in early Tertiary times, and perhaps in Gondwanaland prior to its fragmentation (Nelson, 1981). Its flora is characterised by Gondwanan taxa such as *Gunnera*, *Caltha*, *Coprosma*, *Orites*, *Lomatia* and *Nothofagus*. The alpine flora of Tasmania, particularly, reflects the long climatic stability, and many of the endemic genera and species are found there. It also includes (in common with the Australian Alps) many genera, such as *Ranunculus*, *Epilobium*, *Euphrasia*, *Veronica*, *Mentha* and *Carex*, which have northern hemisphere affinities (Nelson, 1981) and which have undergone their only southern radiations in alpine habitats. As suggested above, these genera have reached Tasmania from the north along mountain migration routes, in some cases aided by long-distance dispersal.

Endemism is much lower in the autochthonous component of the Tasmanian flora. During the Quaternary there has been a broad, low, land connection between Tasmania and the mainland at the times of glacial maxima and sea level minima. This has allowed exchange between the lowland floras of the two regions.

The absence from Tasmania of so many families which occur elsewhere in south-eastern Australia is probably due mainly to the small area of the island and its limited habitat diversity; most of the families now absent probably never occurred there. Some mainland groups, however, may have been eliminated from Tasmania during the climatic fluctuations of the Pleistocene and may not have successfully recolonised. Mistletoes (and mistletoe birds) are absent from Tasmania, probably having been eliminated by cold conditions during glacial times and subsequently prevented from returning by the Bass Strait sea barrier (Barlow, 1981a).



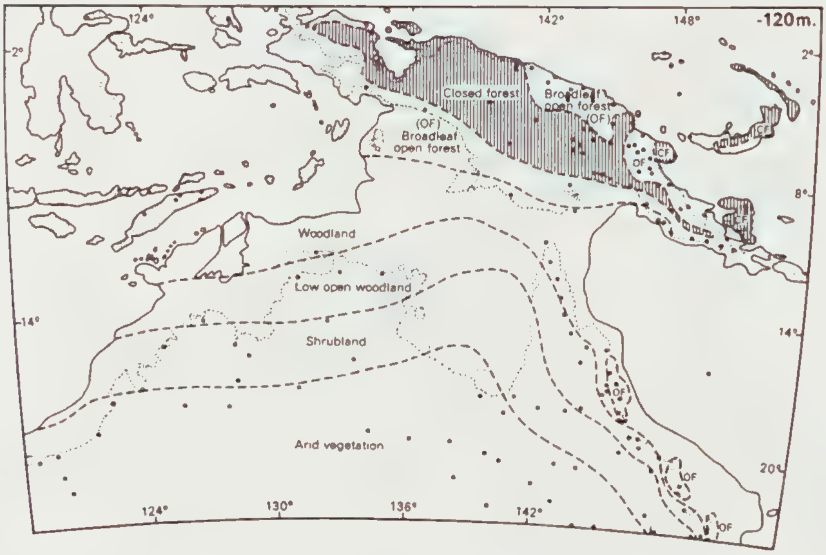
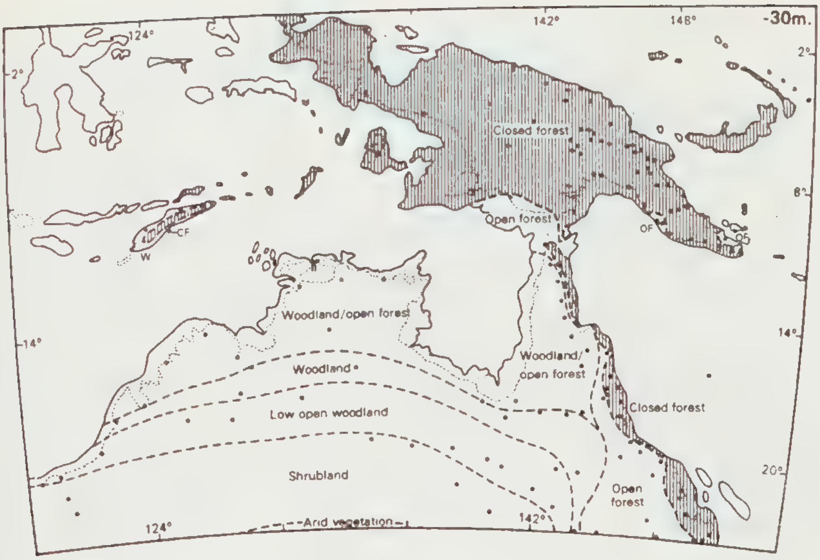


Figure 18 (above). Main structural vegetation types which might have occupied northern Australia, New Guinea and the intervening land about 20 000 years BP. See opposite for legend.

Figure 19 (below). Main structural vegetation types which might have occupied northern Australia, New Guinea and the intervening land about 17 000 to 14 000 years BP. See opposite for legend.



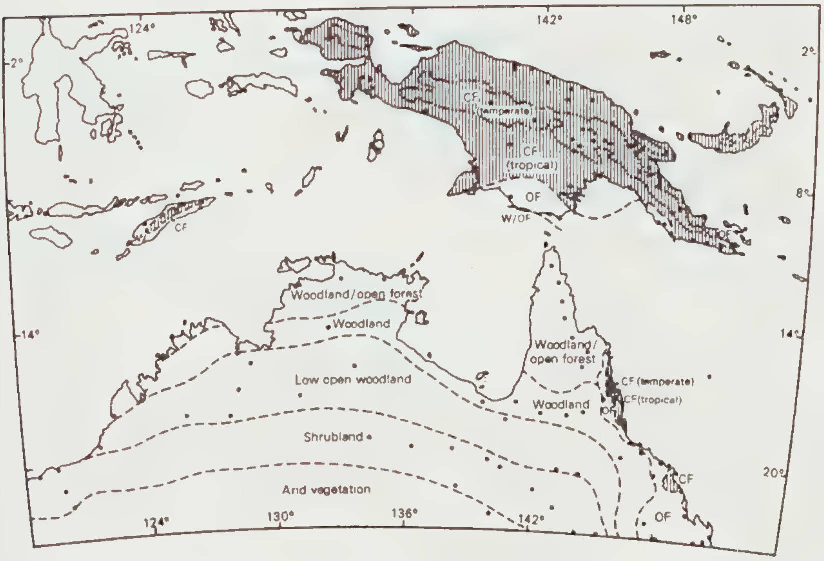


Figure 20 (above). Main structural vegetation types which might have occupied northern Australia, New Guinea and the intervening land about 8 000 years BP.

Figure 21 (below). Main structural vegetation types which occupy northern Australia and New Guinea at present.
Zenithal Equidistant Minimum Error Projection.

.... Tropical/temperate junction
---------- Vegetation zone boundary
________ Estimated coastline
.... Modern coastline
Closed forest.
• Observation station

(After Nix & Kalma, 1972; reprinted by permission from *Bridge and Barrier* 88, 89. © Australian National University)

The dominant Australians — *Eucalyptus* and *Acacia*

Two genera, *Eucalyptus* and *Acacia*, dominate much of Australia's vegetation and contribute greatly to its general character. The history of the Australian flora is in large measure the history of these two genera.

Eucalyptus is not the largest Australian plant genus but it is certainly the most significant, both economically and biologically. The number of species is currently estimated at approximately 500 (Pryor & Johnson, 1981), almost all of which are endemic to Australia. Six Australian species extend to southern New Guinea and a seventh is endemic there. Only three species extend beyond Australia and the New Guinean mainland. One, *E. alba*, is widespread in northern Australia and southern New Guinea and extends to the Lesser Sunda Islands. The other two, *E. urophylla* and *E. deglupta*, are endemic to the Lesser Sunda Islands and New Britain-New Guinea-Sulawesi-Mindanao respectively. It is noteworthy that the total natural distribution of the genus *Eucalyptus* coincides approximately with the total extent of the Australian plate in late Tertiary times as suggested by Audley-Charles et al. (1972).

For phytogeographical reasons alone there can be little doubt that *Eucalyptus* is of ancient Australian origin, although the genus does not appear definitely in the fossil record until the Oligocene (Gill, 1975; Martin, 1981). The eucalypts are not particularly closely related to the scleromorphic shrubby Australian Myrtaceae, nor to arborescent groups such as *Metrosideros* (Pryor & Johnson, 1981), although they apparently share a common ancestry. Detailed studies indicate that the eucalypts may be a diverse group, with the floral operculum having been derived independently in several ways and with significant variations in ovule and seed anatomy as well as in inflorescence structure (Pryor, 1976; Pryor & Johnson, 1981). Because of other unifying factors such as the presence of regularly arranged sterile ovules, it is thought that the eucalypts may have had multiple origins from ancestral stocks which were closely related. This theory has important taxonomic implications, since it may be appropriate to reclassify the eucalypts into several distinct genera. Johnson (1976) has recognised nine such 'informal subgenera' in *Eucalyptus s. lat.*, and Johnson and Briggs (1981) have argued that these groups deserve generic status. Such an approach is strongly supported by the distinct levels of crossability within and between these groups. For largely practical reasons outlined by Pryor (1976) and Johnson (1976), formal taxonomic delimitation of segregate genera has not been completed.

Eucalypts characteristically occur in open forest and woodland associations, and only a few species have been successful in rainforest margins or alpine habitats. In the arid zone they are relatively few and with rare exceptions confined to favourable situations such as stream lines and rocky outcrops. The genus is therefore often associated with the evolution of the scleromorphic autochthonous sub-element of the flora. Pryor and Johnson (1981), however, considered that *Eucalyptus* did not move into older scleromorphic communities until mid-Tertiary time.

The long history of the eucalypts is illustrated by a number of relict species of very limited distribution, and by a striking evolutionary convergence between species of different sections in eastern and western Australia, both in field appearance and in ecological requirements (Pryor, 1976; Pryor & Johnson, 1981). Eucalypts also illustrate the long history of evolution of the Australian scleromorphic flora with fire; the growth habit of these plants makes a major contribution to the flammability of the vegetation. Eucalypts characteristically have narrow pendulous leaves which allow light to penetrate to ground level, drying the copious leaf and bark litter which accumulates. Depending on weather conditions, fires may be confined to the understorey layer or may rage through the crowns intensified by the volatile oils in the leaves. Adaptations in eucalypts include woody capsules which release seeds after fire, thick insulating bark, numerous buds which allow sprouting of large limbs even after intense scorching and, in most species, large woody rootstocks (lignotubers) which are very resistant to aridity as well as to fire. Some of these attributes are common to other genera of the Australian scleromorphic and arid vegetation. It has been suggested that the flammability of the vegetation is an adaptation which promotes rapid heat generation and rapid return to normal temperature, thus preventing destruction of dormant buds (Recher & Christensen, 1981).

Much of the Australian flora may have been pre-adapted to fire by virtue of its adaptations for aridity and nutrient deficiency (Specht, 1981b). Two adaptive strategies are evident; some species are fire tolerant, with the array of protective features mentioned above, while others are fire sensitive but produce large quantities of seed which accumulate either in the soil or in woody fruit and germinate after fire (Recher & Christensen, 1981). *Eucalyptus* and certain other genera (e.g. *Banksia*) have species which fall into each class (Gill, 1975; George, 1976). Long-term successional cycles in scleromorphic communities occur in response to fire (Recher & Christensen, 1981; Specht et al., 1958), with certain species in some cases reappearing in the community as a direct consequence of burning. Some eucalypts will not regenerate in the absence of fire, which may therefore play an important role in maintaining the structure of eucalypt communities in Australia.

The other enormously successful genus in Australia is *Acacia*, which with c. 835 species (Maslin & Hopper, 1981) is the largest in Australia. *Acacia* is well represented in the floras of Africa and tropical America but one characteristic section, *Phyllodinae*, dominates the Australian representation. In this section the leaves, which, in *Acacia*, are primitively bipinnately compound, are reduced in the adult state to expanded petioles, often vertically flattened. This scleromorphic feature is usually explained as an adaptation for aridity.

Acacia is known in the fossil record only since the beginning of the Miocene (Martin, 1981), but it undoubtedly has had a longer Tertiary history in Australia. *Acacia* species occur in nearly all plant formations, including closed forests, but they rise to community dominance in the woody floras of arid and semi-arid regions. In these situations *Acacia* tends to replace *Eucalyptus* as the dominant woodland genus of open habitats, with *Eucalyptus* confined to more favourable sites.

While *Acacia* is ecologically dominant in the arid zone, only 118 of the 835 species (14 per cent) occur there, and endemism to that region is low (Maslin & Hopper, 1981). In comparison, 336 species (40 per cent) occur in the South West Botanical Province of Western Australia, indicating a remarkable diversification within the scleromorphic ecosystems with mediterranean climate.

Acacia probably first radiated in Australia under the warm moist conditions of the middle Tertiary, with some sections later evolving rapidly in southern areas in response to aridity (Maslin & Hopper, 1981). At the present time the tropically derived groups in the arid zone are phenologically in phase with environmental conditions while the groups with southern connections are out of phase (Maconochie, 1979), and appear to be later arrivals.

Origin of the Australian arid zone flora

The arid zone and the derivation of its flora

The arid or eremean zone in Australia is generally defined in terms of the 250 mm (10 in.) isohyet. Thus defined, it comprises more than one third of the Australian land area. In addition, there are other floristic regions in Australia where seasonal aridity is significant. In monsoonal northern Australia, for example, there is a prolonged winter dry season of up to nine months. Burbidge (1960) recognised three large 'interzones' between the Eremean Zone and the other two floristic Zones, Temperate and Tropical. The interzones were characterised by seasonal aridity, and in some cases by heavy soils, and showed a significant representation of arid-adapted plants. In the broad sense, then, more than half of the land area of Australia at the present time is continuously or seasonally arid.

As a consequence, the relationships and evolution of the Australian arid zone flora have received considerable attention. The first studies were purely phytogeographical and generally formed part of the more extensive analyses described earlier. Tate (1888) coined the term 'Eremia', and distinguished two components, Endemic and Exotic, in its flora. Diels (1906) redefined the arid zone under its current spelling 'Eremea' and recognised a Northern Element and an Autochthonous Element in its flora; these correspond to the Exotic and Endemic Elements of Tate. The first of these groups has palaeotropical relationships while the second is purely Australian.

Diels (1906), in what might have been a separate exercise, also classified the flora of the 'Eremean Province' into components based on possible geographical derivations. These included a palaeotropical and cosmopolitan group, mainly in the north, and an Australian group and a littoral group, mainly in the south. Diels also showed an awareness of the overlap between temperate and arid floras in the south-west of the continent. His phytogeographical classification of the arid zone flora seems to have been taken up by Burbidge (1960) with little change. In her analysis she recorded 363 genera of seed plants in the eremean flora, of which 102 were endemic. Of the remainder, 91 genera were also represented in temperate Australia and 81 genera in the adjacent lowland tropics. The cosmopolitan element was represented by 89 genera which were further distributed throughout all regions of Australia.

In terms of phytogeographical analyses, then, there has been little controversy in explaining the derivation of the Australian arid zone flora. Most authors have concluded that it is a young flora, having arisen only after extensive arid conditions were established in relatively recent geological time. It was therefore derived by selection from the pre-existing, highly adapted, total Australian flora. Components of tropical lowland affinity and derivation dominate in the northern part of the Eremea (Burbidge, 1960) and components apparently derived from the autochthonous temperate element dominate in the southern part. The main difficulty has been in the explanation of the cosmopolitan component, including endemic genera in families such as Poaceae, Chenopodiaceae, Brassicaceae, Aizoaceae and Asteraceae, which are among the main constituents of the vegetation of all of the major world deserts. How did these colonisers cross extensive areas of unsuitable and fully occupied territory to become established in the young Australian arid zone?

The solution to the problem has generally been found in the fact that these cosmopolitan families and genera are also well represented in littoral habitats, where salinity and soil type may impose physiological conditions similar to those of deserts. Colonisation of the deserts by such groups may therefore have occurred from coastal habitats, especially in places where the arid zone extends to the coast. Burbidge (1960) placed great emphasis on this hypothesis and suggested that the progenitors of the Australian arid zone vegetation existed on the coastlines from Cretaceous times until the late Tertiary, when the first extensive arid areas were formed.

Age and climatic history

The arid flora is thus widely accepted as being a composite flora derived from adjacent, older plant communities as arid conditions overtook the continent. The major debates have centred on matters of detail. How recent is the arid zone flora? What types of genetic systems have operated in the selection of new biotypes from communities which were already highly adapted? Is there any evidence that the arid zone itself has been a major centre of species radiation for those genera which have colonised it?

Partial answers to these questions have emerged from a number of detailed studies, many of them very recent. The work which set the stage for many of these studies, however, was the celebrated paper by Crocker and Wood (1947). These authors argued that the eremean flora was ultimately derived from a pan-Australian Oligocene flora which existed under conditions of continental low relief, broad climatic zones and high rainfall. From a study of dune formation they postulated cycles of aridity alternating with pluvial phases. During the arid maxima there would have been 'wholesale destruction of native flora' coincident with both the formation of dunes and sand sheets and the retreat of the vegetation cover into refuges, probably in the inland mountain systems. As the climate again became more equable an arid zone vegetation was re-established by migration from the refuges, but only by the adaptively superior biotypes which remained. Migration routes would have been determined by soil type.

Crocker and Wood suggested that there might have been more than one such arid maximum in Recent (post-glacial) times. However they suggested that the last arid maximum, which they put at 10 000 years BP, was the major determinant of the present arid zone flora.

As a result of Crocker and Wood's work it was generally accepted that the arid zone flora of Australia was very recent in origin, having differentiated mainly through the sifting effects of cycles or aridity over the last 50 000 years. Other authors, notably Burbidge (1960), argued from the available fossil and climatological evidence that limited arid conditions may have arisen in the Pliocence (i.e. in the last few million years), but that the extensive occurrence of arid conditions was post-glacial in origin. This conclusion has only been questioned very recently. It should be noted, however, that Crocker and Wood did postulate the existence of an earlier arid flora before their 'Great Arid Period'. Crocker (1957) later suggested that there probably always was an arid zone in Australia, but that its size and position may have changed.

The theory of plate tectonics has provided a simple means of estimating the age of the Australian arid zone. If a steady northward drift of Australia from Antarctica is assumed, then Australia would have entered the subtropical arid belt in Miocene time. On this simplistic basis, the age of extensive aridity in Australia would be at least 15 million years, and it would have impinged on the Australian continent from the north (Beard, 1976).

Bowler (1981) has accepted the view that the present expression of aridity in the Australian landscape dates from events which began in Miocene time. He has, however, questioned the concept that aridity was initiated from the north by Australia's drift into dry subtropical latitudes. He has suggested, from palaeoclimatological evidence, that there has been a northerly displacement of weak sub-tropical anti-cyclonic pressure systems from winter latitudes near 50°S in the Miocene, with the present climatic pattern over Australia being initiated about 2.5 m.y. BP and subsequently intensifying. As a result, aridity would have overtaken the Australian continent from the south rather than the north, and equable, moist, summer rainfall conditions would have given way to seasonally dry conditons. With the continued northward movement of the pressure systems the moisture budget would then have increased again in southern Australia in the last 2.5 million years, leaving the interior with the reduced moisture budget. According to Bowler the present arid zone landforms have a time-frame of 700 000 years but the major wet-dry oscillations of the last 100 000 years have been most significant in determining the landscape.

Recently available palaeobotanical data do indeed suggest that open and perhaps arid plant communities have existed in Australia since the Miocene, whereas in the preceding epochs moist conditions may have prevailed. As described above, the pollen record for many widespread Eocene sites in Australia is consistent with the presence of rainforest types such as *Nothofagus*, *Podocarpus*, Araucariaceae, Cupanieae, *Anacolosa* and *Santalum*, together with an abundance of epiphytic fungi and a great diversity of ferns (Kemp, 1978). The evidence for high humidity at all of the known Eocene sites is very high. There is evidence of a general cooling during the Oligocene, although data are sparse. *Nothofagus* and *Dacrydium* are well represented but diversity in the pollen spectrum is much lower than that of the Eocene (Kemp, 1978), suggesting that cool temperate conditions prevailed. Warm conditions may have prevailed slightly longer in western than in eastern Australia, as tropical rainforest affiliates were present at least until the upper Eocene (Kemp, 1981; Hos, 1975).

As far back as the Eocene there is evidence of localised grassland formation. At the Hale River deposits in central Australia, grass pollen comprises 7 per cent of the total pollen count (Trusswell & Harris, 1981). In samples of Miocene age, grass pollen counts at some sites are as high as 10 per cent and *Casuarina* pollen is sometimes abundant, although cool temperate conditions are generally indicated by the frequent dominance of *Nothofagus* and *Dacrydium*. Lange (1978) recorded from near Woomera an assemblage of fruits assignable to *Eucalyptus*, *Leptospermum*, *Calothamnus*, *Melaleuca–Callistemon* and *Angophora*. The fossil record for the Miocene, while not giving clear evidence of extensive deserts similar to those of today, does indicate the expansion of open forest vegetation and, given the accepted bias of the fossil record towards wet environments, it seems likely that arid conditions were present in the Miocene and perhaps even earlier.

Critical evolutionary studies have led to similar conclusions about the ages of plant groups now common in the arid zone. Carolin (1981), partly from his studies in Caryophyllaceae, has suggested that there has been an arid region in Australia since the break-up of Gondwanaland early in the Tertiary, about 55 m.y. BP. Smith-White and co-workers (1970) have similarly suggested that the complex evolutionary history of *Brachycome* in Australia also favours the existence of some arid conditions throughout the Tertiary. Long evolutionary histories in the arid zone have likewise been suggested for *Triodia* (Jacobs, 1981) and *Calotis* (Stace, 1981). Conversely, significant differentiation has occurred in groups such as the swamp plants of the genus *Sowerbaea* (Stewart & Barlow, 1976b), which have a disjunct circumcoastal distribution. This suggests that a considerable time has elapsed since a former Australia-wide range was disrupted by aridity.

While parts of the eremean flora may therefore be older than formerly thought, this may not be true for all components. Carolin (1981) has maintained that the tropical lowland component may be a recent coloniser of the arid zone, Australia having been in the correct climatic position for this development only since the Pliocene. This view is consistent with the pattern for the onset of aridity in Australia suggested by Bowler (1981).

Even though there is now reasonable evidence for the evolution of an eremean flora in Australia over a period of at least 15 million years, and perhaps twice that period of time, there is remarkably little evidence that the arid zone has functioned as a major centre of species radiation. In an elegant analysis of relationships of *Acacia*, Maslin and Hopper (1981) have indicated that the nearest relatives of adapted arid zone *Acacia* species are mostly to be found in adjacent temperate areas. Numerous parallel lines of adaptation to aridity thus exist, rather than a single line leading to the explosive radiation of a new arid species group. A similar situation almost certainly exists in *Eremophila*, Australian Euphorbieae (Hassall, 1981), *Dodonaea* (West, 1981), Gnaphaliinae (Short, 1981), *Calotis* (Stace, 1981) and other plant groups. It is also paralleled by similar evolutionary patterns in vertebrate and invertebrate animal groups (Baverstock, 1981; Greenslade, 1981). The arid zone thus emerges as an area which has been colonised sucessfully by numerous biotypes selected from adjacent populations growing under more favourable conditions, not as a floristic zone in which internal evolutionary radiation has produced its own characteristic flora.

The most conspicuous group for which this generalisation does not apply is the Chenopodiaceae. Genera such as *Sclerolaena* and *Maireana* (previously known in Australia as *Bassia* and *Kochia* repectively) have apparently radiated widely in arid habitats. In *Atriplex* all the Australian species appear to be derived from a common specialised immigrant ancestral type, except for one coastal species which may be a separate introduction (Parr-Smith, 1981). Several species-clusters have evolved in arid and semi-arid Australia from this ancestral type, all with a distinctive ovule orientation and all with the C_4 dicarboxylic acid metabolism and Kranz anatomy.

The importance of recent cycles of aridity is not completely negated by the extension of the age of the arid zone into earlier Tertiary time. Even an adapted desert flora would have been greatly disrupted by periods of extreme aridity, and the present-day distribution of desert plants is clearly a result of climatic events of the last few thousand years. Cycles of aridity were originally thought to be associated with glacial cycles, such that glacial maxima were pluvial and interglacials were arid. This view is now outmoded (Galloway & Kemp, 1981), and in fact aridity seems often to be associated with lowered temperatures. The time of the last arid maximum in south-eastern Australia is now put at 17 500–16 000 years BP (Bowler, 1978). It may have been followed by a relatively pluvial phase culminating about 3 500 years BP (Gill, 1955), with conditions subsequently moving again towards aridity. In the drier periods the arid flora, especially of stony soils, may have been reduced to mountain refuges and peripheral habitats (Carolin, 1981), with subsequent recolonisation very much dependent on the adaptive potential and competitive abilities of the species involved.

Good evidence for episodic evolution in the arid zone is found in the work of Randell (1970) on the genus *Cassia*. The arid zone species of *Cassia* have been derived from tropical lowland ancestors and have undergone a significant radiation in the Australian inland, coupled with extensive polyploidy at the highest level known for this large pantropical genus. The known diploids occur in or near mountain systems in central and southern Australia which could have been refugia. The most recent range extensions on the arid plains have been by polyploid biotypes, and very extensive hybridisation has occurred where these colonisers have come together. Similarly in the *Eremophila glabra* complex (Ey & Barlow, 1972) diploid biotypes occur in mountain refugia and at the southern margins of the distribution of the complex, while tetraploid and hexaploid biotypes are widespread in the interior.

Dune systems in Australia at the present time are generally stabilised. The last period of widespread dune evolution probably coincided with the last glaciation (Galloway & Kemp, 1981). It extended an edaphic feature which has probably existed for 300 000 years and which has its own adapted plant associations, but it also increased the disjunctions between other associations of the interior. Randell and

Symon (1977), for example, have drawn attention to the disjunct distributions in species of *Cassia* and *Solanum*, determined by the distribution of sand desert.

Mechanisms of evolution

The cytogenetic basis of biotype selection has been examined in a number of arid zone genera. The most common cytoevolutionary syndrome is undoubtedly polyploidy, which has been recorded in most of the genera in which broad surveys have been undertaken. It has been reported in 19 out of 69 taxa in *Eremophila* (Barlow, 1971). In *Cassia* (Randell, 1970) polyploidy was found to be very frequent, with the persistence of polyploid types with reduced sexual fertility achieved through an apomictic system based on adventitious embryony. Polyploidy has also been reported in *Solanum* (Randell & Symon, 1976), *Ptilotus* (Stewart & Barlow, 1976), *Atriplex* (Parr-Smith, 1981), *Brachycome* (Carter, 1978b; Smith-White et al., 1970), *Calotis* (Stace, 1978), *Euphorbia* (Hassall, 1977), *Hibiscus* (Menzel & Martin, 1980), *Goodenia* (Peacock, 1963), *Themeda* (Hayman, 1960), *Erodium* (Carolin, 1958) and *Brunonia* (Peacock & Smith-White, 1978). These genera show a variety of geographical patterns for the polyploid derivatives, and even in some cases the arid zone populations are the residual diploid ones.

Barlow (1969, 1981b) has pointed out that much of the polyploidy in the arid zone flora occurs at the infraspecific level and has thus occurred after the major period of species differentiation in the eremean flora. Polyploidy may be generally associated with the biotype selection which has accompanied the cycles of aridity in Quaternary time, as has already been suggested above for *Cassia* and *Eremophila*. Barlow (1971, 1981b) has also pointed out that in a number of cases the diploid races are found in Western Australia, with polyploids extending eastwards into the interior, suggesting that polyploids have replaced diploids in those areas where climatic fluctuations or stresses may have been greatest.

The role of polyploidy is thought to be one of genetic conservation of new adaptive biotypes (Barlow, 1981b; James, 1981). This is achieved through restriction of gene exchange between different ploidy levels and through its dampening effect on phenotypic segregation. Polyploidy thus allows a new biotype to maximise its production of genetically similar offspring.

Genomic changes other than polyploidy have been reported rarely for arid zone plants. Widespread aneuploidy has been reported in Gnaphaliinae (Asteraceae) by Short (cited by Barlow, 1981b) and in *Calotis* by Stace (1978), who pointed out that aneuploid reduction without compensating change in chiasma frequency may be a device which reduces genetic recombination to an acceptable level for biotypes which have adopted an annual or ephemeral habit. In *Isotoma*, structural change involving the accumulation of reciprocal translocations and a balanced lethal system has led to permanent hybridity (James, 1965, 1970). James has argued that this genetic system has been a response to inbreeding imposed by an increase in aridity in the species range.

Studies in *Brachycome* by Smith-White and colleagues have revealed remarkable cyogenetic adaptations. Extensive dysploidy, from $n=2$ to $n=15$, has occurred in parallel series from a base number of $x=9$ (Smith-White et al., 1970). Infraspecific genomic variation occurs in nucleolar organising regions, in timing of chromatin condensation and by interchange (Watanabe et al., 1975), and through supernumerary chromosomes (Carter & Smith-White, 1972; Carter, 1978a). The most exceptional work, however, has been in the *B. linearifolia* species complex, where a strong correlation has been discovered between change in genome constitution and altered ecological tolerances towards aridity. A diploid race ($2n=8$) occupies coastal habitats on western Eyre Peninsula. Sympatric with it but extending further inland is a quasi-diploid race with $2n=10$ in which there are two different additional chromosomes which are transmitted via the pollen (Carter et al., 1974). This race has a small zone of overlap with a third race, having $2n=12$, in which the additional chromosomes are present in diploid dose (Kyhos et al., 1977). Finally, the race occurring furthest inland is an apparent amphidiploid with $2n=16$, in which the constituent genomes have been derived by hybridisation of the third race just mentioned and a race of *B. dichromosomatica* with $2n=4$. The authors drew attention to a progressive increase in growth vigour of these races and suggested that the successive addition of chromosomes is associated with an increasing tolerance of arid conditions.

The cytogenetic patterns described above clearly illustrate the responses in genetic systems which are involved in adaptation to fluctuating environmental conditions, and particularly to aridity. Their significance under conditions of rapid change, as has occurred in the arid region of Australia in the Quaternary, may be especially great. However it has been pointed out by Barlow (1981b) that gross alterations in the genome are not essential for the conservation of differentiating biotypes, and that the incidence of such changes in the arid zone may be no greater than in other ecological situations or in other periods of time.

Pollination and breeding systems

Adaptation for arid conditions has involved some predictable shifts in the frequencies of the various pollination mechanisms. Keighery (1981) made a general analysis of the eremean flora of Western Australia in comparison with that of adjacent temperate and tropical regions. He reported a general increase in wind- and bee-pollination in the transition from temperate to eremean habitats. Bird-pollination declined dramatically, and pollination by non-flying mammals disappeared completely, even though both of these pollination syndromes are important in the Australian flora as a whole (Armstrong, 1979). In the latter case the shift is due to a general absence of the pollinators, but this is not true of nectivorous birds. Among entomophilous types there is a general decline in all pollinators except bees and bee flies. Keighery pointed out that these pollinator shifts are consistent with a shift to smaller flowers, which may be more economical with respect to nectar production and water conservation.

Keighery (1981) also noted a shift towards self-compatibility in the eremean flora. He suggested that the unpredictable environment of the arid zone has had a second effect in addition to restricting the diversity of pollinators and pollination syndromes. The second effect is a shift to self-compatibility as a 'fail-safe' reproductive system countering pollinator unpredictability, even though the species involved are generally adapted for outbreeding.

The Australian flora — a national heritage

The uniqueness of the Australian flora is clearly a matter of degree. As a whole, the flora can be seen primarily as part of an extensive southern hemisphere flora in which certain features are rather uniform. For example, its dominant temperate flowering trees are evergreen, whereas those of the northern hemisphere are mostly deciduous. This feature has been discussed by Axelrod (1966), who attributed the difference to the palaeoclimatic conditions under which northern and southern temperate floras evolved. The southern flora lacks the conifers which dominate cooler plant associations in the north. In respects such as this, the Australian flora is a typical sample of southern hemisphere vegetation.

A closer study reveals the unique characteristics of the flora, extending to virtually all plant communities. Our arid zone is not matched in extent by any other desert region south of the equator. It has a unique combination of cosmopolitan and ancient Australian plants, many of which are susceptible to replacement by introduced aliens better adapted phenologically, and many of which cannot withstand intensive pastoral activity. It differs from other deserts in having very few succulent xerophytes; most of its woody plants are drought resisters with a physiological capacity to endure dehydration; and it has a beautiful ephemeral flora which is rarely seen and includes threatened species (Specht et al., 1974). The alpine habitat in Australia is very limited in extent, and carries a rare combination of ancient southern plants and adapted Australian ones distributed above a tree line which is remarkably low because of the lack of conifers or frost-hardy angiosperms in Australia. Elsewhere in eastern and south eastern Australia, and especially in south western Australia, the scleromorphic floras of poor soils and seasonal habitats are bewildering in their diversity; they are matched in diversity (but not in composition) only by the Cape flora of South Africa (Johnson & Briggs, 1981). As mentioned above, endemism in these floras is very high, so that numerous species are confined to very small areas.

Because of a growing community awareness of the special character of our plant associations, a number of effective conservation measures have been taken. Up to now, however, much of this action has been directed towards protection of selected communities in selected locations, often associated with spectacular scenery or with recreational sites. The conservation of whole floristic elements as a whole should be considered as a matter of principle, especially where we recognise them to be relict with a slender tenure on survival. This approach is already being made, for example, in Western Australia (Anon., 1974). Further action must follow as our understanding of the composition, history and relationships of the surviving natural plant communities continues to grow.

The need for this action can be illustrated by example. The temperate and subtropical rainforests of eastern Australia survive today in a number of isolated pockets scattered along the coast and ranges, and their total area has been considerably reduced both by logging and by clearing for pastoral activity. According to our former view of Australian biogeography, these communities would have been seen as modern invaders (in the sense of geological time) of the Australian flora—almost as prehistoric aliens supplanting our truly Australian vegetation. We now see these rainforests as the remnants, in Australia, of the ancient Gondwanan flora which covered the entire continent when it was still attached to Antarctica sixty million years ago. They are the surviving residue of the primitive stocks from which the bulk of the modern Australian flora has been derived. This residue comprises the taxa which have undergone the least evolutionary change and includes some of the most primitive genera of flowering plants still surviving in the world. These are the most ancient Australians still surviving. Perhaps, with such an understanding of the history of these forests and with awareness of their intrinsic beauty, we should consider, as a matter of national pride, conserving all that remains of them.

The Australian flora, as we see it today, thus tells the story of a hundred million years of history of Australia as a southern land mass. The alien plants which have become naturalised so widely since European settlement are legitimately included in the Australian flora. Their impact on the flora, however great, has nevertheless occurred almost instantaneously in terms of the long history of colonisation of the continent by plants.

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AN INTRODUCTION TO THE SYSTEM OF CLASSIFICATION USED IN THE *FLORA OF AUSTRALIA*

A. Kanis

Floras and the classification of plants

Floras are works of reference about plants, arranged in systematic categories ('taxa'), of defined geographical areas. Because they vary in the amount of detail included as well as the size and complexity of the area covered, they can differ considerably in size and format. In handbooks and more comprehensive floras particular attention is given to the principal means of plant identification, viz. keys and comparable descriptions of taxa, largely based on morphological characters. The taxon most commonly recognised, and therefore emphasised in Floras, is the *species* ('kind' or 'sort'). In works of a critical nature, almost equivalent attention may be given to such infraspecific categories as *subspecies* and *varietas* ('variety'). No doubt this is for the practical reason that the information most frequently required is about species and subordinate taxa.

In accordance with general principles of classification, the basic taxonomic categories are grouped into larger units: from many rather concretely defined ones to fewer more generalised and therefore more abstract ones. The arrangement of individual plants and populations into larger categories, on the basis of degrees of similarity and of discontinuity in variation, results in a hierarchical system. The information presented in floras is arranged in accordance with such a system, because it facilitates comparisons if similar taxa are treated in close proximity.

Not all taxa that may be distinguished above the rank of species are of equal interest. Certain ranks are traditionally given greater prominence than others in floras, sometimes to the complete exclusion of intermediate ones. The next category of practical importance above species is that of *genus*. Although essentially more theoretical in concept, genera are often more readily recognised than their composite taxa. A generic name (always treated as a Latin singular noun though frequently of Greek or other derivation) forms the first part of a binary name which is given to every species. The second part is the so-called 'specific epithet', which is usually an adjective. To denote a subspecies or a variety a third element, usually a second adjective, is added to the name of the relevant species. As a result the very nomenclature of plants reflects a systematic arrangement, at least from the generic level downwards.

The present concepts of genus, species and variety can be traced back to the writings of the Swedish botanist Carl von Linné (1707–1778) better known as Linnaeus, although they were adapted and defined, rather than invented, by him. Many of the genera and subordinate taxa recognised by Linnaeus have since been widened or, more often, narrowed in their circumscription, but the great majority of these have survived to form the core of all subsequent systems of classification. For ranks above that of genus, Linnaeus deliberately used an artificial system of orders and classes based on a minimum of arbitrarily chosen floral characters such as the number of stamens and pistils ('sexual system'). He regarded this as the most practical solution for classifying the avalanche of new plants reaching scientists in his day from remote, newly explored parts of the world.

The influence of the Linnaean system was so great that it largely discouraged the development and use of alternatives for over half a century. As knowledge of the world's flora increased, however, botanists became better equipped to design so-called 'natural systems'. These have been based on similarities and differences in as many characters as possible, both vegetative and reproductive. The recognition of 'natural orders' was strongly promoted in the latter part of the 18th Century by some French botanists, of whom Antoine Laurent de Jussieu (1748–1836) was the most influential. One of the very first floras in which genera were arranged by natural orders was also the first concerned with the Australian region, viz. Robert Brown's *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* (1810). During the 19th Century it became customary to replace the term 'natural order' by the alternative *familia* ('family'), first promoted by another Frenchman, Michel Adanson (1727–1806). Some families such as *Apiaceae* (*Umbelliferae*), *Brassicaceae* (*Cruciferae*) and *Poaceae* (*Gramineae*) were already recognised as natural groups by some of Linnaeus' predecessors and are therefore older than the formal category itself. Family names are of practical use because they can be remembered more easily, being rather fewer in number than their included genera. This advantage, however, is somewhat eroded by the trend to divide large 'traditional' families into more homogeneous but smaller ones. Attempts to place all genera in appropriate families have not been completely successful, but such problems as still exist will probably be solved eventually by modern methods of research.

For the last hundred years or so, the term *ordo* ('order') has been used for the rank above family in the hierarchical classification. Traditionally, orders have been given scant attention in floras. In other taxonomic literature, however, there has been an upsurge of interest in the arrangement of families and higher ranks within the Flowering Plants. Among the systems proposed more recently, there is an increasing similarity in the concepts of these taxa. As a result, orders may eventually take over the role of memory pegs from families.

The next major taxonomic category above order is that of *classis* ('class'). The question which group of taxa constitutes a class could be expected to be a subject of much controversy. In the Flowering Plants, however, there is a remarkable and long-standing agreement among botanists to recognise only two classes, sometimes regarded as subclasses, viz. *Liliopsida* (=*Monocotyledoneae*) and *Magnoliopsida* (=*Dicotyledoneae*). Flowering Plants as a whole, previously also known as *Angiospermae*, or *Anthophyta s. str.*, are ranked sometimes as a *subdivisio* (Ehrendorfer, 1971), but more usually as a *divisio* ('division'), for which the modern name *Magnoliophyta* has been introduced (Cronquist et al., 1966). This taxon in turn may be placed in subregnum *Embryobionta* (Cronquist et al., 1966), the next higher category, which is perhaps more widely known under the older name *Cormophyta*. Finally, the ultimate rank of *regnum* ('kingdom') traditionally accommodates all plants (*Vegetabilia* or *Plantae s. lat.*) as opposed to animals (*Animalia*).

The primary division of all organisms into plants and animals, as reflected in the traditional partitioning of biology into botany and zoology, is no longer regarded as satisfactory from a theoretical point of view. There appears to be a more fundamental difference between those organisms that lack a distinct cellular nucleus (*Prokaryota*) and those that do possess such an organelle (*Eukaryota*). The former group includes only the *Schizophyta* or Bacteria and Blue-Green Algae (=kingdom *Monera*, Raven et al., 1981). Modern authors prefer to divide the eukaryote organisms into a number of kingdoms or subkingdoms, some accommodating those traditionally regarded as plants. The *Protista s. lat.* (=*Protobionta* or *Thallophyta*) may include the autotrophic Algae (=*Phycophyta*) as well as the heterotrophic Fungi (=*Mycophyta*). On the other hand, both *Protista s. str.* and (higher) Fungi may be treated as equivalent taxa (kingdoms, Raven et al., 1981), possibly of the same rank as the *Embryobionta*, or plants in the narrow sense. Apart from the *Magnoliophyta*, the *Embryobionta* accommodates the following divisions (after Cronquist et al., 1966): *Bryophyta* (Mosses and Liverworts), *Psilophyta* (Whisk Ferns), *Lycopodiophyta* (=*Lycophyta* or Clubmosses), *Equisetophyta* (=*Sphenophyta* or Horsetails), *Polypodiophyta* (=*Pterophyta* or Ferns) and *Pinophytina* (=*Gymnospermae*). Traditionally, *Magnoliophyta* and *Pinophyta* have been treated together as *Spermatophyta* (=*Phanerogamae* or Seed Plants), whereas *Embryobionta,* excluding *Bryophyta* but including *Pteridophyta* (Ferns and Fern Allies), have been grouped together as *Tracheophyta* (Vascular Plants). In many floras the treatment is restricted to the *Magnoliophyta* or *Spermatophyta*. The *Pteridophyta* are often included in smaller floras of temperate regions, but otherwise are usually treated, like *Bryophyta* and *Protobionta*, in independent and specialised works. It is intended that the *Flora of Australia* will ultimately cover all plants known to grow naturally in the region except the Bacteria.

To illustrate what has been discussed in the preceding paragraphs, the hierarchy of taxonomic terms is presented in Table 3 with appropriate names at each rank for *Acacia pycnantha* Benth. From the family level downwards it is customary to provide the name of the original author(s) ('authority'), often in an abbreviated form, after the taxonomic name. These are often useful, particularly as different authors have sometimes used the same name inadvertently for different taxa at the same level, either as independently coined names ('homonyms') or as a result of misinterpretation ('misapplied names'). A name in brackets indicates an earlier author who may have used the same taxonomic name at a different rank in the hierarchy. In the case of an infra-generic name, the author may have used the second or third element of that name originally in combination with the name of another genus or species respectively.

The background of phylogenetic classification

When de Jussieu proposed a natural system for the classification of plants in his *Genera Plantarum* (1789), he probably did so as a true representative of the so-called 'idealistic morphologists'. It is unlikely that he considered the distinguishing characters of the respective groups of plants to be the result of an evolutionary process, as such hypotheses hardly entered scientific thought until the end of the 18th Century. Contemporary biologists saw it as their task to recognise the essential (or 'archetypal') characters of taxa, thought to be obscured in Nature by a multitude of variants. In their opinion a natural system of classification of all creatures, should reflect the 'Grand Design' (in a theological or philosophical sense) fundamental to Nature.

The first theory to challenge the idea of immutability of species with some success was proposed by the Parisian professor Jean Monnet de Lamarck in his *Philosophie Zoologique* (1809). It was Charles Darwin's *On the Origin of Species by Means of Natural Selection* (1859), however, that profoundly changed biological and philosophical thinking. Natural systems acquired a new dimension through evolutionary theories, and were increasingly regarded as models reflecting degrees of actual relationship through common descent. Species within a single genus were considered to have diverged from each other later and/or more slowly (and therefore to a lesser degree) than genera within a family. The same principle was believed to apply to other taxonomic ranks. A stepped hierarchical system cannot, however, adequately reflect all stages of gradual diversification at any one time. Therefore a decision to recognise a particular group as a distinct taxon at a particular rank will always be somewhat arbitrary. In certain groups, taxa at the specific level may be clearly isolated from each other by discontinuities in character variation, whereas relevant taxa

Table 3. Hierarchy of taxonomic categories: major ones in capitals, the most commonly used intermediate ones in lower case. The example shows the classification of the Golden Wattle. Names from subregnum down to divisio after Cronquist et al. (1966), from classis to familia after Cronquist (1981). The name for the subseries was not validly published as Bentham did not assign it to a particular rank at any time.

REGNUM (kingdom)	*Eukaryota* (Organisms of nucleate cells)
Subregnum	*Embryobionta* (Stem Plants)
DIVISIO (division)	*Magnoliophyta* (Flowering Plants)
Subdivisio	
CLASSIS (class)	*Magnoliopsida* (Dicotyledons)
Subclassis	*Rosidae*
ORDO (order)	*Fabales* (Leguminous Plants)
Subordo	
FAMILIA (family)	*Mimosaceae* R.Br. (1814)
Subfamilia	
Tribus (tribe)	*Acacieae* (Reichb.) Endl. (1841)
Subtribus	
GENUS	*Acacia* Miller (1754)
Subgenus	*Acacia* subg. *Heterophyllum* Vassal (1972)
Sectio (section)	*Acacia* sect. *Phyllodineae* DC. (1825)
Series	*Acacia* ser. *Uninerves* Benth. (1864)
Subseries	[*Acacia* 'Racemosae' Benth. (1842, 1864)]
SPECIES (kind)	*Acacia pycnantha* Benth. (1842)
Subspecies	
VARIETAS (variety)	*Acacia pycnantha* Benth. var. *pycnantha (1864)*

of higher rank may be difficult to segregate and circumscribe. On the other hand certain genera may be easy to define and agree upon, but their subdivision into species may be difficult because relevant natural populations show overlapping ranges of variation in a number of characters. Such difficulties may well appear in floras through keys to identification that do not always give satisfactory results.

Darwin's ideas undoubtedly had an impact on the natural system of plant classification developed by George Bentham and Joseph Hooker. Published in their *Genera Plantarum* (1862–1883), this system was most influential until the beginning of the 20th Century. It is interesting to note that the only comprehensive flora yet completed for the Australian region as a whole, Bentham's *Flora Australiensis* (1863–1878), was one of the first great floras written in that period.

From the beginning of the 20th Century onwards, genetic research has provided a deeper insight into the nature of morphologically-based taxa, particularly at generic and subordinate levels. It has become clear that it is of limited use to recognise formal categories, such as subvarieties, forms and even subforms, as was fashionable in some 'schools' until quite recently. On the other hand, varieties and higher taxa, originally only recognised because of apparent similarities of of the constituent individuals ('phenotypes'), were usually shown to have a common genetic potential ('gene pool'). Encouraged by these results, botanists have attempted to provide definitions for the lower taxa, in particular the species, by using more objective criteria, e.g. the degree of fertility between individuals or populations. They have, however, failed to find any criteria that are suitable for universal application and it seems as yet impossible to remove subjectivity from taxonomic practice.

Theories on the evolution of life, as well as developments in other biological disciplines, have certainly influenced the thinking of taxonomists. Most plant taxa, however, are still recognised and defined primarily by gross morphological characters ('alpha taxonomy'). It is possible nowadays to test similarities and discontinuities by using additional criteria derived from such disciplines as anatomy, palynology, embryology, cytology, phytochemistry and genetics ('omega taxonomy'). Taxonomists usually take into account significant results from these areas of research when circumscribing taxa and designing systems of classification. If all taxonomic studies were made on such a comprehensive scale, however, it would slow down a more balanced accumulation of taxonomic knowledge over the widest possible front. A comprehensive system of classification even in a rather preliminary stage, is of more immediate use for urgently needed floras.

Natural and phylogenetic systems of classification

The question remains whether 'natural systems' can ever be improved to the point where they reflect adequately the course of the evolution of organisms ('phylogeny'). The following factors act counter to any attempts to achieve this aim:

(1) *Inadequacy of the fossil plant record* Although the fossil record is relatively good for some categories of organisms—mostly animal groups such as molluscs and vertebrates—it is rather poor for others, particularly many plant groups. Consequently, direct evidence for the pathways of evolution is largely lacking in a group like the Flowering Plants and may never become available. Assumptions about past development must therefore be based mainly on evidence derived from living representatives. Unfortunately, some botanists have been tempted to present 'genealogical trees' in which all the key positions of the branching system are occupied by recent taxa. Such systems should be regarded as pseudo-phylogenetic. If one adopts the model of a phylogenetic tree, it is only justifiable to regard it as buried by the sands of time, with the living species just visible as extremities of the finest twigs (Fig. 22).

(2) *Convergent evolution* If evolution were a process of continuing divergence only, one could expect to approach the phylogenetic ideal gradually by simply improving the traditional systems based on degrees of similarity. It is evident, however, that widely different groups can become more similar through convergent evolution, at least in a number of characters which may be conspicuous. To return to the imagery used above: it is probable that adjacent branch tips are more recent offshoots of a single larger branch than of those that are further apart. This assumption may not be confirmed, however, once the sand is removed, since twigs of different branches may have grown towards each other and may have become closer than twigs of any single branch developing either divergently or in parallel. Convergent developments have certainly caused misinterpretations in the past: e.g. the *Magnoliopsida* (Dicotyledons) with fused corolla lobes were formerly united as the subclass *Sympetalae* but are now regarded as a rather artificial group of families and orders of disparate origins. In other words, certain taxa have reached a similar stage in their evolution with regard to a few correlated characters, although they need not be considered by other criteria as closely related. To overcome the problem of classifying such artificial, often polyphyletic taxa ('grades'), numerical methods have been developed that enable us to assess as many similarities and dissimilarities as possible. When making such assessments, it is important to determine as far as possible which characters are 'primitive' and which are 'advanced', as only the latter can give positive indications of relative distances of relationships. The (re-)evaluation of taxa on this wider basis results in groups with a high probability of being monophyletic ('clades'). This approach appears to affect traditional systems more drastically at the higher levels where a greater degree of uncertainty has always existed.

In conclusion, it appears that the most improved 'natural system' of classification also provides the most probable model of actual evolution that can be deduced. One cannot clearly distinguish between 'natural' and 'phylogenetic' systems. A schematic presentation of a modern phylogenetic system of classification of the *Magnoliophyta* by the Swedish taxonomist Rolf Dahlgren (1980) is reproduced in Figure 22. In this diagram, the 'tips of the branches' have been grouped into larger units (orders and superorders) by cladistic methods. Their relative proximity is an expression of similarity or dissimilarity in a range of characters.

The system used in the *Flora of Australia*

As explained above, the nomenclature of plants itself imposes on Floras a systematic grouping from the generic level down, but a particular system is usually adopted for the placement of genera into families. The choice of a system does not necessarily determine the sequence of genera and families, since these may be arranged alphabetically or according to assumed relationships at any or all of these levels. A sequence according to degrees of similarity appears preferable, particularly in works which deal with many representatives of any one taxon. Taxonomic relationships would be best expressed in a multi-dimensional scheme, whereas the treatment in a book necessarily follows a more arbitrary linear sequence. In practice this does not appear to be a major disadvantage, while it could also be argued that any systematic arrangement of taxa in a Flora is primarily an expediency, theoretical considerations being of little interest to most users. Nevertheless, it would appear undesirable to choose a system that is clearly out of date.

The Editorial Committee for the *Flora of Australia* decided in 1979 that a sequential system should be adopted, so that the families could be assigned to particular volumes from the beginning. For the Flowering Plants their choice fell on the latest version of Arthur Cronquist's system then being prepared for publication (Cronquist, 1981), since it was thought that it would be the most modern published by the time the first volumes of the Flora were to appear. Cronquist's system, as relevant to Australia, is given on the front endpapers of this introductory volume, together with a schedule for the Flora. A systematic arrangement of taxa other than *Magnoliophyta* will be decided at a later date.

Current systems of Magnoliophyta

For readers interested in the latest developments in this field, a comparison is presented here of the most recent systems of classification designed to accommodate the whole of the subdivision *Magnoliophyta*. Such a discussion must be limited in scope in this introductory chapter. It is not warranted to compare systems that are of historical interest only and that have been discussed at length in other publications. As a starting point, the latest edition of Volume 2 of *A. Engler's Syllabus der Pflanzenfamilien* (Melchior, 1964) has been chosen. This work surveyed the more important systems from 1940 onwards, down to the level of order, and provided a comprehensive bibliography of relevant literature.

A comparison of modern classification systems of *Magnoliophyta* was published more recently in tabular form by Kenneth M. Becker (1973). Choosing Arthur Cronquist's systematic sequence (1968) as a basis he made a concordance down to family level of the systems of Armen Takhtajan (1966, 1968), Robert Thorne (1968), Hans Melchior (1964) and John Hutchinson (1959, 1969) together with the historically interesting one by George Bentham and Joseph D. Hooker (1862–1883). He also accounted for the additional families accepted by H. K. Airy Shaw (1966). A slightly modified version of Hutchinson's system has since been published posthumously (1973), while Takhtajan (1980) has also brought out a revised version. Both Cronquist and Thorne have prepared updated editions of their systems, and Dahlgren recently proposed a new system that has already appeared in two editions (1975, 1980).

The families of Flowering Plants after H. K. Airy Shaw

From its seventh edition onwards, H. K. Airy Shaw has revised J. C. Willis's *A Dictionary of the Flowering Plants and Ferns* (7th edn, 1966; 8th edn, 1973). He assigned most genera of the relevant taxa (including Gymnosperms!) to a family. Airy Shaw listed and described a relatively high number of segregate families and usually indicated relationships at that level as understood by him. He did not present an original system, however, as the families were consistently correlated with the higher categories of the now rather obsolete system of Adolf Engler in *Syllabus der Pflanzenfamilien* (7th edn, 1912).

Airy Shaw recognised 247 families of Flowering Plants that are known to be represented in Australia by indigenous species. Of these, 26 families (10.5%) were not recognised as such by Melchior (1964), Hutchinson (1973) or Cronquist (1981), including *Bambusaceae* and *Ternstroemiaceae*, which he regarded as of uncertain status. A further 24 families (9.7%) have been accepted by only one other of these authors and 16 (6.5%) by two of them. All 66 'controversial' families are listed in the first column of Table 4, adjusted to the left-hand margin. Their taxonomic positions—as far as their Australian representatives are concerned—according to the other three authors are listed in parallel columns, with alternative positions indicated by indented names.

Compared with the systems of Dahlgren (1980), Takhtajan (1980) and Thorne (1981) (Table 8), 18 of the 26 families (7.3% of the total) were still recognised only by Airy Shaw. The other eight families were accepted by those three as follows: *Limoniaceae*, *Sambucaceae*, *Tetracarpaeaceae*, *Thunbergiaceae* (by Dahlgren),

Table 4. Families of Flowering Plants with representative taxa indigenous in Australia as recognised by four authors, but not regarded as distinct by all four. Alternative taxonomic positions of segregate families are shown by indented names, some queried (?), some highlighted (!).

H.K. Airy Shaw (1973)	**J. Hutchinson (1973)**	**A. Cronquist (1981)**	**H. Melchior ('Engler' 1964)**
Aegialitidaceae Lincz.	(not accounted for)	Plumbaginaceae	Plumbaginaceae—Staticeae
Myrsinaceae	Aegicerataceae Blume	Myrsinaceae	Myrsinaceae—Aegiceratoideae
Amaryllidaceae J. St. Hil.	Amaryllidaceae	Liliaceae(!)	Amaryllidaceae
Anarthriaceae Cutler & Airy Shaw	Restionaceae	Restionaceae	Restionaceae—Anarthrieae
Apostasiaceae Lindley	Apostasiaceae Blume	Orchidaceae	Orchidaceae—Apostasieae
Thymelaeaceae—Aquilarioideae	Aquilariaceae R. Br.	Thymelaeaceae	Thymelaeaceae—Aquilarioideae
Atherospermataceae R. Br.	Monimiaceae	Monimiaceae	Monimiaceae—Atherospermatoideae
Avicenniaceae Endl.	Verbenaceae	Verbenaceae	Verbenaceae—Avicennioideae
Bambusaceae Nakai (*stat. dub.*)	Poaceae—Bambuseae	Poaceae	Gramineae—Bambusoideae
Barringtoniaceae Rudolphi	Barringtoniaceae	Lecythidaceae	Lecythidaceae—Planchonioideae
Baueraceae Lindley	Baueraceae	Cunoniaceae(!)	Saxifragaceae—Baueroideae
Bischofiaceae (Muell.Arg.) Airy Shaw	Euphorbiaceae	Euphorbiaceae—('Bischofficae')	
Blepharocaryaceae Airy Shaw	Anacardiaceae	Sapindaceae(?)	Anacardiaceae—Rhoideae
Leguminosae—Caesalpinioideae	Caesalpiniaceae R. Br.	Caesalpiniaceae	Leguminosae—Caesalpinioideae
Cartonemataceae Pichon	Cartonemataceae	Commelinaceae	Commelinaceae
(see 'Dicrastylidaceae')	Chloanthaceae Hutch.	Verbenaceae	Verbenaceae—Chloanthoideae
Chrysobalanaceae R. Br.	Rosaceae(!)	Chrysobalanaceae	Chrysobalanaceae
Cleomaceae (Pax) Airy Shaw	Cleomaceae Horan.	Capparaceae	Capparaceae—Cleomoideae
Cochlospermaceae Planchon	Cochlospermaceae	Bixaceae(!)	Cochlospermaceae
Costaceae Nakai	Zingiberaceae	Costaceae	Zingiberaceae—Costoideae
Cuscutaceae Dumort.	Cuscutaceae	Cuscutaceae	Convolvulaceae—Cuscutoideae
Cymodoceaceae N. Taylor	Zanichelliaceae	Cymodoceaceae	Zanichelliaceae—Cymodoceae
Davidsoniaceae Bange	Cunoniaceae(!)	Davidsoniaceae	Davidsoniaceae
'Dicrastylidaceae', *nom. illeg.*	(see Chloanthaceae)		
Donatiaceae Dostál	Donatiaceae	Donatiaceae	Stylidiaceae—Donatioideae
Dysphaniaceae Pax	Dysphaniaceae	Chenopodiaceae(!)	Dysphaniaceae
Ecdeiocoleaceae Cutler & Airy Shaw	Restionaceae	Restionaceae	Restionaceae—Anarthrieae
Ehretiaceae Lindley	Ehretiaceae Mart.	Boraginaceae	Boraginaceae—Ehretioideae
Elaeocarpaceae DC.	Tiliaceae(!)	Elaeocarpaceae	Elaeocarpaceae
Emblingiaceae (Pax) Airy Shaw	Capparaceae	Polygalaceae(!)	Capparaceae—Emblingioideae

Eremosynaceae Takht.	Eremosynaceae	Saxifragaceae	Saxifragaceae—Eremosynoideae
Escalloniaceae Dumort.	Escalloniaceae R. Br.	Grossulariaceae(!)	Saxifragaceae—Escallonioideae
Leguminosae—Papilionoideae	Fabaceae Lindley	Fabaceae	Leguminosae—Faboideae
Flindersiaceae (Engler) Airy Shaw	Rutaceae—Cusparieae	Rutaceae(?)	Rutaceae—Flindersioideae
Gunneraceae Meissner	Halorag(id)aceae	Gunneraceae	Haloragaceae—Gunneroideae
Gyrocarpaceae Dumort.	Hernandiaceae	Hernandiaceae	Hernandiaceae—Gyrocarpoideae
Hanguanaceae Airy Shaw	Flagellariaceae	Hanguanaceae	Flagellariaceae(?)
Ranunculaceae—Helleboreae	Helleboraceae Loisel	Ranunculaceae	Ranunculaceae—Helleboroideae
Celastraceae	Hippocrateaceae	Hippocrateaceae	Hippocrateaceae
Centrolepidaceae	Centrolepidaceae	Hydatellaceae Hamann (1976)	Centrolepidaceae—Trituriceae
Hydrocotylaceae Hylander	Apiaceae	Apiaceae	Umbelliferae—Hydrocotyloideae
Guttiferae	Hypericaceae Juss.	Clusiaceae	Guttiferae—Hypericoideae
Hypoxidaceae R. Br.	Hypoxidaceae	Liliaceae(!)	Hypoxidaceae
Idiospermaceae S.T. Blake	Idiospermaceae	Idiospermaceae	Calycanthaceae
Caryophyllaceae—Paronychioideae	Illecebraceae R. Br.	Caryophyllaceae	Caryophyllaceae—Paronychioideae
Leeaceae Dumort.	Vitaceae(!)	Leeaceae	Leeaceae
Limnocharitaceae Takht.	Butomaceae	Limnocharitaceae	Butomaceae—Limnocharitoideae
Limoniaceae Lincz.	Plumbaginaceae	Plumbaginaceae	Plumbaginaceae—Staticeae
Campanulaceae—Lobelioideae	Lobeliaceae R. Br.	Campanulaceae	Campanulaceae—Lobelioideae
Memecylaceae DC.	Melastomataceae	Melastomataceae	Melastomataceae—Memecyloideae
Leguminosae—Mimosoideae	Mimosaceae R. Br.	Mimosaceae	Leguminosae—Mimosoideae
Aizoaceae—Mollugineae	Molluginaceae Hutch.	Molluginaceae	Molluginaceae
Naucleaceae Wernham	Rubiaceae	Rubiaceae	Rubiaceae—Naucleae
Nelumbonaceae Dumort.	Nymphaeaceae	Nelumbonaceae	Nymphaeaceae—Nelumbonoideae
Nypaceae Tralau	Arecaceae—Phytelephantineae	Arecaceae	Palmae—Nypoideae
Peperomiaceae Wettst.	Piperaceae	Piperaceae	Piperaceae
Periplocaceae Schltr.	Periplocaceae	Asclepiadaceae(?)	Asclepiadaceae—Periplocoideae
Philesiaceae	Petermanniaceae Hutch.	Smilacaceae	Liliaceae—Luzuriagoideae
Phytolaccaceae—Rivineae	Petiveriaceae Agardh	Phytolaccaceae	Phytolaccaceae—Rivineae
Philesiaceae Dumort.	Philesiaceae	Smilacaceae	Liliaceae—Luzuriagoideae
Posidoniaceae Lotsy	Posidoniaceae	Posidoniaceae	Potamogetonaceae—Posidonieae
Potaliaceae Mart.	Potaliaceae	Loganiaceae	Loganiaceae—Potalieae
Epacridaceae—Prionoteae	Prionotaceae Hutch.	Epacridaceae	Epacridaceae—Prionoteae
Ruppiaceae Hutch.	Ruppiaceae Hutch.	Ruppiaceae	Potamogetonaceae—Potamogetoneae
Solanaceae—Salpiglossideae	Salpiglossidaceae Hutch.	Solanaceae	Solanaceae—Salpiglossideae
Sambucaceae Link	Caprifoliaceae	Caprifoliaceae	Caprifoliaceae—Sambuceae

Table 4 (cont.)

H.K. Airy Shaw (1973)	**J. Hutchinson (1973)**	**A. Cronquist (1981)**	**H. Melchior ('Engler' 1964)**
Actinidiaceae—Saurauieae	Saurauiaceae J. Agardh	Actinidiaceae	Actinidiaceae—Saurauioideae
Siphonodontaceae Tardieu	Siphonodontaceae	Celastraceae	Celastraceae—Siphonodontoideae
Smilacaceae Vent.	Smilacaceae	Smilacaceae	Liliaceae—Smilacoideae
Sphenocleaceae DC.	Campanulaceae(!)	Sphenocleaceae	Sphenocleaceae
Sphenostemonaceae P. Royen & Airy Shaw	Trimeniaceae(!)	Aquifoliaceae(?)	Aquifoliaceae(?)
Spigeliaceae Mart.	Spigeliaceae	Loganiaceae	Loganiaceae—Spigelieae
Stilaginaceae Agardh	Euphorbiaceae	Euphorbiaceae	Euphorbiaceae—Phyllantheae
Strychnaceae Link	Strychnaceae	Loganiaceae	Loganiaceae—Strychneae
Stylobasiaceae J. Agardh	Rosaceae(!)	Surianaceae(!)	Chrysobalanaceae(?)—Stylobasieae
Surianaceae Arn.	Simaroubaceae	Surianaceae	Simaroubaceae—Surianoideae
Ternstroemiaceae Mirbel (*stat. dub.*)	Theaceae	Theaceae	Theaceae—Ternstroemioideae
Tetracarpaeaceae Nakai	Escalloniaceae(!)	Saxifragaceae	Saxifragaceae—Tetracarpaeoideae
Tetragoniaceae Nakai	Aizoaceae	Aizoaceae	Aizoaceae—Tetragonioideae
Tetramelaceae (Warb.) Airy Shaw	Datiscaceae	Datiscaceae	Datiscaceae—Tetrameleae
Burmanniaceae—Thismieae	Thismiaceae J. Agardh	Burmanniaceae	Burmanniaceae—Thismieae
Thunbergiaceae Tieghem	Acanthaceae	Acanthaceae	Acanthaceae—Thunbergioideae
Ericaceae—Gaultherieae	Vacciniaceae Gray	Ericaceae	Ericaceae—Vaccinioideae
Viscaceae Miquel	Loranthaceae	Viscaceae	Loranthaceae—Viscoideae
Xanthophyllaceae Gagnep.	Polygalaceae	Xanthophyllaceae	Polygalaceae—Xanthophylleae
Zosteraceae Dumort.	Zosteraceae	Zosteraceae	Potamogetonaceae—Zosteraceae

Ecdeiocoleaceae, *Stylobasiaceae* (by Takhtajan), *Emblingiaceae* (by Dahlgren and Takhtajan) and *Sphenostemonaceae* (by Dahlgren, Takhtajan and Thorne). Of the families not accepted by any of the other six authors discussed here, the following were originally proposed by Airy Shaw: *Anarthriaceae*, *Bischofiaceae*, *Blepharocaryaceae*, *Flindersiaceae* and *Tetramelaceae*.

Five of Airy Shaw's 'controversial' families were described by him and his collaborators as new taxa, whereas another five were raised by him to this rank for the first time. The remaining 56 families had been proposed before, some early in the 19th Century, but generally have not been accepted at that level. However, it is clear from the list of alternative taxa accepted by Melchior (Table 4) that most of these have been treated at some time as subfamilies or tribes. In the eighth edition of Willis' *Dictionary*, Airy Shaw included for the first time four families recently described, viz. *Aegialitidaceae*, *Idiospermaceae*, *Limoniaceae* and *Sphenostemonaceae*, whereas *Petermanniaceae*, accepted in the seventh edition, was relegated to *Philesiaceae*.

Table 4 is of wider interest because all four systems compared therein are relatively well-known through handbooks. Hutchinson is the only one who agreed with Airy Shaw in accepting the following eight families: *Barringtoniaceae*, *Cartonemataceae*, *Chloanthaceae* ('*Dicrastylidaceae*'), *Cleomaceae*, *Periplocaceae*, *Potaliaceae*, *Spigeliaceae* and *Strychnaceae*. Of the others accepted by Airy Shaw, *Xanthophyllaceae* has been supported as a distinct family only by Cronquist, *Idiospermaceae* by Hutchinson and Cronquist, *Dysphaniaceae* by Melchior and Hutchinson, and *Sphenocleaceae* by Melchior and Cronquist. Other families in the Table such as *Hanguanaceae*, that would appear to fall into any of these categories, were in fact supported by Dahlgren, Takhtajan and/or Thorne. On the other hand, Airy Shaw did not accept two families recognised by Melchior, Hutchinson and Cronquist, viz. *Hippocrateaceae* (which he referred to *Celastraceae*, as did Dahlgren, Thorne and Takhtajan) and *Molluginaceae* referred by him to *Aizoaceae*, (supported only by Thorne). Finally, it is noteworthy that Airy Shaw agreed with Melchior (as well as Thorne and Takhtajan) in maintaining *Fabaceae s. lat.* (=*Leguminosae*) as a single family, whereas Hutchinson and Cronquist (as well as Dahlgren) recognised *Caesalpiniaceae* and *Mimosaceae* next to *Fabaceae s. str.* as families in their own right.

J. Hutchinson's system

The first edition of John Hutchinson's *The Families of Flowering Plants arranged according to a new system based on their probable phylogeny* (1926, 1934) was unorthodox in many respects. The ultimate format of his system was reached in the second edition (1959), being only slightly updated in the posthumous third edition (1973). Although the author certainly considered contemporary developments in phylogenetic literature, his system can no longer be regarded as 'modern' as he relied largely on a personal, intuitive approach. His conclusions have not attracted many followers, but there is no doubt that his publications have done much to stimulate others.

Hutchinson ranked the Flowering Plants as a 'phylum', a term not acceptable under the *International Code of Botanical Nomenclature*, normally regarded as synonymous with Divisio. The *Dicotyledones* and *Monocotyledones* were classed as 'subphyla' and were subdivided into five 'divisions', the latter groups perhaps comparable with the subclasses of other authors. Within the *Monocotyledones* he recognised: (1) *Calyciferae*, with distinct whorls of sepaloid and petaloid tepals (many aquatic plants), (2) *Corolliferae*, with petaloid tepals only, and (3) *Glumiflorae*, without coloured tepals ('grass-like' plants). Most subsequent authors have regarded this subdivision as too artificial, but Hutchinson's ideas on the lower ranking taxa have usually been received more sympathetically. In some more recent systems (Dahlgren, 1980; Takhtajan, 1980) an even more radical treatment has been advocated for some of the 'corolliferous' orders through recognition of more segregate families.

Hutchinson's system has been criticised for the concepts of his 'divisions' in the Dicotyledons, viz. (1) *Lignosae*, covering the predominantly woody families, and (2) *Herbaceae*, containing the non-woody ones. Such a subdivision was promoted by some of Linnaeus' predecessors (e.g. Robert Morison, 1620–1683), but not again for at least two centuries. Modern authors regard this grouping as highly artificial, resulting in phylogenetically improbable 'grades' rather than scientifically desirable 'clades'. Hutchinson's approach resulted in wide separation of families and orders such as *Magnoliales* and *Ran(uncul)ales*, which are usually considered closely related. In some instances he split traditional orders, regarded as quite natural entities by others, enabling him to allocate relevant families to his two 'divisions'. Further examples of such pairs of woody versus non-woody taxa are: *Capparales*/*Brassicales*, *Myrsinales*/*Primulales*, *Cunoniales*/*Saxifragales*, *Myrtales*/*Onagrales*, *Araliales*/*Umbellales* (*Apiales*, *s. str.*), *Verbenales*/*Boraginales* and *Rubiales*/*Gentianales*. Nineteen other segregate orders are unique, as far as Australia is concerned, to his system. Hutchinson also used more traditionally formed names for the following orders: *Graminales* (=*Poales*), *Guttiferales* (=*Clusiales*), *Leguminales* (=*Fabales*), *Palmales* (=*Arecales*), *Personales* (=*Scrophulariales s. str.*). Of his world-wide total of 111 orders of Flowering Plants, 99 are represented in Australia by native taxa: many more than have been recognised in the other systems discussed here (Table 4).

According to the latest version of Hutchinson's system the number of families of Flowering Plants with indigenous representatives in Australia is 230. Like Airy Shaw, he accepted quite a number of mostly small, segregate families (Table 4), but between his 44 'controversial' ones (19.1% of his total) and Airy Shaw's 66 there were only 26 in common. Of these only eight families have not been accepted by any of the other five authors discussed above. Another eight families were recognised exclusively by Hutchinson, viz. *Aquilariaceae*, *Helleboraceae*, *Illecebraceae*, *Petiveriaceae*, *Prionotaceae*, *Salpiglossidaceae*, *Saurauiaceae* and *Vacciniaceae*, while five families are supported only by Dahlgren, viz. *Aegicerataceae*, *Hypericaceae*, *Lobeliaceae*, *Petermanniaceae* and *Thismiaceae*. Of the five or six families proposed by himself, only *Ruppiaceae* was supported by Airy Shaw as well as by Cronquist and Takhtajan, whereas *Molluginaceae* was recognised by all except Airy Shaw and Thorne.

Five families, represented in Australia by segregates according to Airy Shaw's concepts, should themselves be listed as indigenous following Hutchinson's system, viz. *Butomaceae* (in lieu of *Limnocharitaceae*), *Caprifoliaceae* (in lieu of *Sambucaceae*), *Cornaceae* (for *Corokia*), *Datiscaceae* (in lieu of *Tetramelaceae*) and *Theaceae* (in lieu of *Ternstroemiaceae*). Six families have either been segregated since the second edition of his *Families* or replace larger ones as far as Australia is concerned: *Idiospermaceae* (1973, in lieu of *Calycanthaceae*), *Dysphaniaceae* (1973, next to *Chenopodiaceae*), *Barringtoniaceae* (1969, in lieu of *Lecythidaceae*), *Cleomaceae* (1969, away from *Capparidaceae*), *Prionotaceae* (1969, between *Epacridaceae* and *Ericaceae*) and *Salpiglossidaceae* (1969, near *Solanaceae*). Unfortunately, in 1973 he accepted Airy Shaw's replacement of the name *Chloanthaceae* by the illegitimate *Dicrastylidaceae*.

Hutchinson remained unique among modern authors in not recognising *Chrysobalanaceae* (in *Rosaceae*), *Davidsoniaceae* (in *Cunoniaceae*) and *Elaeocarpaceae* (in *Tiliaceae*), whereas he subsequently received support for including *Leeaceae* in *Vitaceae* (from Dahlgren and Thorne) and *Sphenocleaceae* in *Campanulaceae* (from Dahlgren, Thorne, and recently Takhtajan). Remarkable placings were *Sphenostemon* in *Trimeniaceae*, rather than the traditional *Aquifoliaceae* or the modern *Sphenostemonaceae*, and *Tetracarpaea* in *Escalloniaceae* (recently also by Takhtajan) rather than *Saxifragaceae* (Melchior, Cronquist, Thorne) or *Tetracarpaeaceae* (Airy Shaw, Dahlgren). The relatively recent *Aegialitidaceae* was not accounted for by Hutchinson, either directly or indirectly. Finally, *Emblingiaceae* was not mentioned in the various editions of the *Families*, but was placed under *Capparaceae* in his *The Genera of Flowering Plants* (Vol. 2, 1967) as well as, ambiguously, under *Flacourtiaceae* in his later *Evolution and Phylogeny* (1969).

A. Engler's 'Syllabus'

Adolf Engler's *Syllabus der Pflanzenfamilien* first appeared in 1892, under a different title (Engler, 1892). The system presented in this work had probably succeeded that by Bentham and Hooker as the most influential by the turn of the century. Engler updated his ideas in nine subsequent editions up to 1924, after 1912 with the assistance of Ernst Gilg. An eleventh edition, edited by Engler's successor Ludwig Diels, was published in 1936. The twelfth edition was thoroughly rewritten and appeared in two volumes, the first edited by Hans Melchior and Erich Werdermann (1954), the second only by Melchior (1964). This version was quite modern in that it took into account many contemporary ideas on phylogeny. Furthermore, the system presented was actually a team effort by several staff members of the Berlin herbarium rather than one man's synthesis. It may be regarded as conservative, however, rather than radical, even for the time of its publication. The second volume dealt only with the Flowering Plants (*Angiospermae*) which were ranked as a division ('Abteilung'). Of the two classes recognised, *Dicotyledoneae* and *Monocotyledoneae*, only the former was subdivided into two subclasses, viz. *Archichlamideae* (incl. *Apetalae* & *Choripetalae*) and *Sympetalae* (*Metachlamydeae*). These two subclasses have been regarded by more recent authors as artificial, polyphyletic taxa ('grades').

The Englerian system has been most influential at order level. A total of 62 orders was recognised world-wide, and of these 52 have indigenous representatives in Australia, a relatively low number (Table 5). Of the Australian orders 19 were further divided into 53 suborders, making a total of 86 suborders and undivided orders, which approaches Hutchinson's number of 99 more closely. Apart from maintaining relatively large concepts at the rank of order, Engler's system also preserved some traditional names discarded by subsequent authors, viz. *Centrospermae* (± *Caryophyllales*), *Guttiferales* (± *Dilleniales* & *Theales*), *Myrtiflorae* (*Myrtales s. lat.*, incl. *Haloragales*, *Lecythidales*, *Rhizophorales*), *Tubiflorae* (± *Callitrichales*, *Lamiales*, *Scrophulariales* & *Solanales*), *Umbelliflorae* (± *Apiales*, *Araliales* and *Cornales*), *Helobieae*, *Alismatales*, *Hydrocharitales* & *Najadales*), *Liliiflorae* (*Liliales s. lat.*), *Microspermae* (*Orchidales s. lat.*), *Principes* (*Arecales*), *Scitamineae* (*Zingiberales*), *Spathiflorae* (*Arales*). Two of these, *Myrtiflorae* and *Liliiflorae*, have been reintroduced more recently for taxa of a higher rank, viz. superorders (Thorne, 1968 etc.; Dahlgren, 1980). Other large, heterogeneous orders in the Englerian system were *Geraniales*, *Rosales*, *Rutales* and *Commelinales*, whereas *Sarraceniales* and *Papaverales* have been replaced, as far as their Australian representatives are concerned, by *Nepenthales* and *Capparales* according to most subsequent authors.

According to Melchior's edition of the *Syllabus*, the total number of families of flowering plants indigenous in Australia was 200. Family concepts have been kept relatively large, so that many of Airy Shaw's and Hutchinson's segregate families have been recognised only as subfamilies or tribes. Of the 85 'controversial' smaller families in Table 4, Melchior accepted only 11 at that rank, and none of these could be regarded as highly controversial at the time. *Dysphaniaceae*, *Hippocrateaceae* and *Sphenocleaceae* were not recognised as distinct families by Dahlgren, Takhtajan or

Thorne, *Hypoxidaceae* by Takhtajan or Thorne, and *Leeaceae* by Dahlgren or Thorne. As can be seen from the Table, Cronquist also rejected two of these families, as well as *Amaryllidaceae* (also by Thorne) and *Cochlospermaceae* (also by Takhtajan).

If Melchior's larger concepts are accepted, the following families should be regarded as indigenous in Australia instead of the segregates accepted by Airy Shaw and Hutchinson: *Calycanthaceae* (in lieu of *Idiospermaceae*), *Lecythidaceae* (in lieu of *Barringtoniaceae*) and *Saxifragaceae* (in lieu of *Baueraceae*, *Eremosynaceae* and *Escalloniaceae*). Melchior agreed with Hutchinson in regarding the inclusive families *Butomaceae*, *Caprifoliaceae*, *Cornaceae*, *Datiscaceae* and *Theaceae* as indigenous.

Of the seven systems discussed here, Melchior's was unique in not recognising either *Petermanniaceae* or *Philesiaceae* (both in *Liliaceae-Luzuriagoideae*), as well as *Posidoniaceae* and *Zosteraceae* (both as subfamilies in *Potamogetonaceae*). Melchior has been supported only by Hutchinson in rejecting *Costaceae* (in *Zingiberaceae*), *Cymodoceaceae* (in *Zanichelliaceae*), *Gunneraceae* (in *Haloragaceae*), *Nelumbonaceae* (in *Nymphaeaceae*) and *Viscaceae* (in *Loranthaceae*). The endemic genus *Stylobasium* was placed, somewhat unusually, in *Chrysobalanaceae* (cf. *Rosaceae* after Hutchinson) rather than the mono-generic *Stylobasiaceae* (Airy Shaw, Takhtajan), *Surianaceae* (Cronquist), or *Sapindaceae* (Dahlgren, Thorne).

Table 5. The number of families and higher taxa of *Magnoliophyta* with indigenous representatives in Australia according to seven recent authors.

	Thorne (1981)	**Melchior (1964)**	**Cronquist (1981)**	**Takhtajan (1980)**	**Dahlgren (1980)**	**Hutchinson (1973)**	**AiryShaw (1973)**
Classes	1	2	2	2	1	2 ('subphyla')	
Subclasses (+ undivided classes)	2	2 (1)	11	10	2	5 ('divisions')	
Superorders	26	—	—	27	30	—	
Orders	51	52	69	74	84	99	
Suborders (+ undivided orders)	53 (33)	53 (33)	—	55 (50)	—	—	
Families	190	200	215	219	234	230	247

A. Cronquist's system

The first version of Arthur Cronquist's system (1957) was restricted to the Dicotyledons, but an extended treatment later appeared as a book entitled *The Evolution and Classification of Flowering Plants* (1968). As stated above, the 1981 edition of his system has been chosen as the framework for the *Flora of Australia*. Although original in some respects, the system is mostly a synthesis and is somewhat conservative in its treatment of controversial groups such as the *Liliales s. lat*. He acknowledges both Engler's *Syllabus* and the ideas of Walter Zimmermann (1892–1980) and Armen Takhtajan as a basis for the development of his ideas.

Cronquist treats the Flowering Plants as Divisio *Magnoliophyta*, with two traditional classes under the modern names *Magnoliopsida* and *Liliopsida*. He has, however, abandoned the Englerian subclasses completely, adopting instead a break-down into eleven subclasses not unlike that of Takhtajan's system. In the *Magnoliopsida* he recognises: (1) *Magnoliidae*, (2) *Hamamelidae*, (3) *Caryophyllidae*, (4) *Dilleniidae*, (5) *Rosidae*, (6) *Asteridae* (one less than Takhtajan). The *Liliopsida* are subdivided into: (1) *Alismatidae*, (2) *Arecidae*, (3) *Commelinidae*, (4) *Zingiberidae* and (5) *Liliidae* (two more than Takhtajan, 1980). All these subclasses embrace so-called primitive as well as advanced orders and are presented as probable phylogenetic alliances ('clades'). Unlike Takhtajan and other modern authors such as Dahlgren and Thorne, Cronquist does not use the taxon 'superorder'.

According to Cronquist's latest system, the Flowering Plants are represented in Australia by 69 indigenous orders, an average number compared with other systems (Table 5). Three orders are recognised only by Cronquist, viz. *Callitrichales*, *Lecythidales* and *Linales*, and seven others have been supported by only one other author (Table 6). The traditional order *Plantaginales* has not been upheld by other modern authors such as Dahlgren; Takhtajan and Thorne. Cronquist has a relatively narrow concept of some orders, e.g. *Gentianales* (excl. *Rubiales* and *Menyanthaceae*), *Geraniales* (excl. *Linales* and *Zygophyllaceae s. lat.*) and *Commelinales* (excl. *Restionales*). Relatively large concepts are maintained for the *Rosales* (incl. *Cunoniales*, *Saxifragales* and *Pittosporales* p.p.), *Sapindales* (incl. *Rutales* and *Zygophyllaceae*), *Scrophulariales* (incl. *Bignoniales* and *Oleales*), *Violales* (incl. *Cucurbitales*, *Passiflorales*, *Tamaricales* and *Cochlospermaceae*), *Cyperales* (incl. *Poales*), *Liliales* (incl. *Smilacales* and several segregate orders of Hutchinson and Dahlgren), *Najadales* (incl. *Zosterales*) and *Orchidales* (incl. *Burmanniales*). In the 1981 edition of his system, he has replaced *Araliales* by *Apiales* and *Polemoniales* by *Solanales*, whereas 5 new orders have been added: *Callitrichales*, *Hydatellales*, *Laurales*, *Nepenthales* and *Rhizophorales*.

The position of the following families according to Cronquist's system is unusual: *Austrobaileyaceae* (in *Magnoliales* rather than *Laurales*), *Balanopaceae* (in *Fagales* rather than *Balanopales*), *Balanophoraceae* (in *Santalales* rather than *Balanophorales*), *Boraginaceae* (in *Lamiales* rather than *Boraginales*) *Dichapetalaceae* (in *Celastrales* rather than *Euphorbiales*), *Droseraceae* (in *Nepenthales*), *Elaeagnaceae* (in *Proteales* rather than *Rhamnales* or *Elaeagnales*), *Gyrostemonaceae* (in *Batales*), *Nelumbonaceae* (in *Nymphaeales* rather than *Nelumbonales*), *Thymelaeaceae* (in *Myrtales* rather than *Thymelaeales*) and *Tremandraceae* (in *Polygalales*, like Takhtajan, rather than *Pittosporales*).

The total number of Flowering Plant families indigenous in Australia is 215 according to Cronquist's latest system, approximately an average number (Table 5). Of the 85 'controversial' families listed in Table 4 he accepts 27: 14 in agreement with Airy Shaw, 5 with Hutchinson and 7 with both, whereas he adds only the very recently described *Hydatellaceae*. Of these 27 families, *Hippocrateaceae*, *Idiosperm-*

Table 6. An approximate concordance of subclasses (Roman numerals) and superorders (Arabic numerals) recognised in four current systems. Similarly named taxa in the respective systems do not necessarily cover the same orders and families and in some cases the discrepancies are considerable. Takhtajan's *Juglandanae* are represented in Australia by introduced species only. Dahlgren's superorder *Loasiflorae* does not occur in Australia and is not listed.

Cronquist (1981)	**Takhtajan (1980)**	**Thorne (1981)**	**Dahlgren (1980)**
A. **MAGNOLIOPSIDA**	A. **MAGNOLIATAE**	I. **Annonidae**	I. **Magnoliidae**
I. **Magnoliidae**	I. **Magnoliidae**		
	1. Magnolianae	1. Annoniflorae *p.p.*	1. Magnoliiflorae
	2. Rafflesianae	3. Rafflesiiflorae	
	3. Nymphaeanae	2. Nymphaeiflorae	2. Nymphaeiflorae
	II. **Ranunculidae**		
	4. Ranunculanae	1. Annoniflorae *p.p.*	3. Ranunculiflorae
II. **Hamamelidae**	III. **Hamamelidae**		
	5. Hamamelidanae	12. Hamamelidiflorae	
	(6. Juglandanae)	(10. Rutiflorae *p.p.*)	
III. **Caryophyllidae**	IV. **Caryophyllidae**		
	7. Caryophyllanae	5. Chenopodiiflorae	4. Caryophylliflorae
			5. Polygoniflorae
	8. Plumbaginanae	4. Theiflorae *p.p.*	
IV. **Dilleniidae**	V. **Dilleniidae**		
	9. Dillenianae	4. Theiflorae *p.p.*	8. Theiflorae
		8. Violiflorae	7. Violiflorae
		(1976: Cistiflorae)	
			6. Malviflorae *p.p.*
	10. Ericanae	4. Theiflorae *p.p.*	9. Primuliflorae
			21. Corniflorae *p.p.*
	11. Malvanae	9. Malviflorae *p.p.*	6. Malviflorae *p.p.*
V. **Rosidae**	VI. **Rosidae**		
	12. Rosanae	13. Rosiflorae	10. Rosiflorae *p.p.*
			11. Podostemiflorae
			12. Fabiflorae
	13. Myrtanae	14. Myrtiflorae	14. Myrtiflorae
	14. Rutanae	10. Rutiflorae	15. Rutiflorae
		6. Geraniiflorae	15. Rutiflorae
	15. Aralianae	18. Corniflorae	18. Araliiflorae
			21. Corniflorae *p.p.*
	16. Celastranae	7. Santaliflorae	16. Santaliflorae
			17. Balanophoriflorae
	17. Proteanae	11. Proteiflorae	13. Proteiflorae
VI. **Asteridae**	VII. **Asteridae**		
	18. Gentiananae	15. Gentianiflorae	22. Gentianiflorae
	19. Lamianae	16. Lamiiflorae	23. Lamiiflorae
		17. Solaniflorae	20. Solaniflorae
	20. Asteranae	19. Asteriflorae	19. Asteriflorae

Table 6 (cont.)

Cronquist (1981)	Takhtajan (1980)	Thorne (1981)	Dahlgren (1980)
B. **LILIOPSIDA**	B. **LILIATAE**	II. **Liliidae**	II. **Liliidae**
VII. **Alismatidae**	VIII. **Alism(at)idae**		
	21. Alismatanae	22. Alismatiflorae	24. Alismatiflorae
VIII. **Arecidae**	X. **Arecidae**		
	27. Arecanae	23. Areciflorae	30. Areciflorae
	28. Aranae	24. Ariflorae	26. Ariflorae
		25. Typhiflorae	27. Liliiflorae *p.p.*
IX. **Commelinidae**	IX. **Liliidae**		
	24. Juncanae	26. Commeliniflorae *p.p.*	29. Commeliniflorae
	25. Commelinanae	26. Commeliniflorae *p.p.*	28. Zingiberiflorae
X. **Zingiberidae**			
	26. Zingiberanae	26. Commeliniflorae *p.p.*	28. Zingiberiflorae
XI. **Liliidae**			
	22. Triuridanae	21. Triuridiflorae	25. Triuridiflorae
	23. Lilianae	20. Liliiflorae	27. Liliiflorae *p.p.*

aceae, *Sphenocleaceae* and *Xanthophyllaceae* were not upheld by Dahlgren, Takhtajan or Thorne; *Donatiaceae*, *Leeaceae*, *Limnocharitaceae* and *Ruppiaceae* were supported only by Takhtajan; and *Caesalpiniaceae*, *Fabaceae s. str.* and *Mimosaceae* in that rank only by Dahlgren.

According to Cronquist the following families are indigenous in Australia and should not be replaced by segregates: *Bixaceae* (in lieu of *Cochlospermaceae*, supported by Takhtajan), *Grossulariaceae* (in lieu of *Escalloniaceae*), *Lecythidaceae*, *Saxifragaceae* (both in agreement with Melchior), *Caprifoliaceae*, *Datiscaceae* and *Theaceae* (all three in agreement with Melchior and Hutchinson). Compared with his edition of 1968, *Celastraceae* now includes *Siphonodontaceae*, but several segregate families are additional or replace others, viz. *Cabombaceae* (next to *Nymphaeaceae*), *Caesalpiniaceae*, *Fabaceae s. str.* and *Mimosaceae* (in lieu of *Leguminosae*), *Donatiaceae* (next to *Stylidiaceae*), *Gyrostemonaceae* (away from *Phytolaccaceae*), *Idiospermaceae* (in lieu of *Calycanthaceae*), *Viscaceae* (next to *Loranthaceae*), *Cymodoceaceae* and *Posidoniaceae* (next to *Zosteraceae*), *Hanguanaceae* (away from *Flagellariaceae*) and *Hydatellaceae* (away from *Centrolepidaceae*).

Cronquist's system is remarkable for not recognising *Amaryllidaceae* and *Hypoxidaceae* (both in *Liliaceae*, supported by Thorne), *Cochlospermaceae* (in *Bixaceae*, supported by Takhtajan) and *Dysphaniaceae* (in *Chenopodiaceae*, supported by Dahlgren, Takhtajan and Thorne). Noteworthy also is his placing of *Baueraceae* in *Cunoniaceae* (supported by Takhtajan), *Blepharocaryaceae* doubtfully in *Sapindaceae* (rather than *Anacardiaceae* after Takhtajan and Thorne), *Emblingiaceae* in *Polygalaceae* (rather than *Capparaceae*), *Escalloniaceae* in *Grossulariaceae* and *Stylobasiaceae* in *Surianaceae*.

A. Takhtajan's 'Outline'

Since the early 1940s Armen Takhtajan has published some 20 contributions on the evolution and palaeogeography of plants. The majority of these, written in Russian, are not easily followed by most English readers, but a few major ones have appeared in other European languages. The first to be translated into English (1953) concerned a phylogenetic system for the higher ranks of the *Cormophyta*, in which the class *Angiospermae* was not subdivided beyond the subclasses *Dicotyledones* and *Monocotyledones*.

Takhtajan's first publication to have an impact outside the U. S. S. R. was *Die Evolution der Angiospermen* (1959). In that book he proposed an original grouping of orders into superorders (13 in the *Dicotyledonae*, 5 in the *Monocotyledonae*). Takhtajan used traditional names that had been used at the lower rank of order in the Englerian system. His ideas subsequently developed greatly and were presented in English under the title *Flowering Plants, Origin and Dispersal* (1969). In this book he treated *Magnoliatae* (Dicots) and *Liliatae* (Monocots) as classes, dividing the former into 7 subclasses and 15 superorders and the latter into 4 subclasses and 5 superorders. Besides recognising additional taxa between the ranks of class and order, he discarded all traditional names at these levels, choosing new ones based on generic names with standardised suffixes. This format was not changed significantly in the most recent *Outline* (1980), although the number of subclasses in the *Liliatae* were reduced by one (*Commelinidae* into *Liliidae*), and eight new superorders were added (5 in *Magnoliatae* and 3 in *Liliatae*) (Table 6). Of the new total of 28 superorders only the *Juglandanae*, a relatively small one, is not represented in Australia by native species. Takhtajan's subclasses were very similar to those of Cronquist, particularly in their respective systems of 1969 and 1968, a circumstance no doubt reflecting consultation between them. Takhtajan's superorders, on the other hand, probably influenced the development of the systems of Thorne and Dahlgren, who may well have provided him with some ideas in return. Takhtajan alone of these four authors used both ranks to indicate probable phylogenetic relationships ('clades').

Of the 74 indigenous orders recognised by Takhtajan, 15 segregates have not been adopted by Cronquist. Of these 15, three were unique to his system, viz. *Begoniales*, *Connarales* and *Smilacales*. On the other hand, 10 orders used in Cronquist's system were not recognised by Takhtajan (Table 7). In comparing Takhtajan's latest system with his previous version (1969), it appears that four orders were discontinued, viz. *Cucurbitales*, *Passiflorales* (both in *Violales*); *Hydrocharitales* (in *Alismatales*) and *Iridales* (now in *Liliales* and *Burmanniales*). Apart from some minor changes in the sequence of orders, there were five additional orders, viz. *Araliales*, *Balanophorales*; *Burmanniales*, *Hydatellales* and *Smilacales*.

The following families were remarkable for their placement in Takhtajan's system: *Actinidiaceae* (in *Ericales* rather than *Theales*), *Boraginaceae* (in *Polemoniales* rather than *Lamiales*), *Datiscaceae* (in *Begoniales* rather than *Violales*), *Dichapetalaceae* (in *Euphorbiales* rather than *Celastrales*), *Frankeniaceae* (in *Tamaricales* rather than *Violales*). Some families were notable for being transferred to other orders between the editions of 1969 and 1980: *Cardiopteridaceae* (from *Santalales* to *Celastrales*), *Droseraceae* (from *Nepenthales* to *Saxifragales*), *Emblingiaceae* (from *Capparales* to *Sapindales*), *Malpighiaceae* (from *Geraniales* to *Polygalales*), *Nitrariaceae* and *Zygophyllaceae* (from *Geraniales* to *Rutales*), *Stylobasiaceae* (from *Rutales* to *Sapindales*); *Hanguanaceae* (from *Restionales* to *Liliales*).

Takhtajan recognised 16 segregate families not recognised by Cronquist (Table 7) and no longer accepted 9 of Cronquist's families. Further, the following families have been synonymised by Takhtajan since 1969: *Brunoniaceae* (in *Goodeniaceae*), *Cochlospermaceae* (in *Bixaceae*), *Gyrocarpaceae* (in *Hernandiaceae*), *Hippocrateaceae* (in *Celastraceae*), *Hypericaceae* (in *Clusiaceae*), *Lobeliaceae* (in *Campanulaceae*), *Saurauriaceae* (in *Actinidiaceae*), *Sparganiaceae* (in *Typhaceae*), *Sphenocleaceae* (in *Campanulaceae*), *Tetracarpaeaceae* (in *Escalloniaceae*), *Tetragoniaceae* (in *Aizoaceae*). Finally, Takhtajan agreed with Cronquist in the recent acceptance of *Viscaceae* as a family distict from *Loranthaceae*.

R. F. Thorne's 'Synopsis'

Robert F. Thorne kindly allowed the use of the latest version of his system (1981) so that it could be discussed in this introductory chapter. He has written a number of earlier papers on relationships within certain groups of Flowering Plants as well as on general evolutionary problems. Thorne has published two papers on a phylogenetic classification of the angiosperms: the first was a synopsis with a brief introduction (1968), the second a much more elaborate treatment (1976). Thorne considers modern phytochemical research to be an important addition to morphological knowledge. His system is original in several respects, but there is a superficial resemblance to Melchior's 'conservative' one, as it does not follow the general trend of fragmentation of orders and families. He uses the ranks of suborder and subfamily to indicate distinction as well as close relationships between taxa. Thorne admits that his ideas are subject to constant change, which may explain why he has not yet published them more extensively. Although his system has great merit, its very instability renders it less suitable as a basis for a medium- to long-term project such as the *Flora of Australia*.

Thorne regards the *Angiospermae* (or '*Annonopsida*') as a class, and consequently he treats the *Dicotyledoneae* ('*Annonidae*') and *Monocotyledoneae* ('*Liliidae*') as subclasses, which are immediately subdivided into 19 and 7 superorders respectively. The 26 superorders are comparable to those of Takhtajan and Dahlgren (Table 5). In Thorne's 1976 system the respective figures were 16 (without *Nymphaeiflorae*, *Proteiflorae* and *Solaniflorae*) and 5 (without *Triuridiflorae* and *Typhiflorae*). His earlier *Cistiflorae* has been renamed *Violiflorae* in 1981. Superorders in the various editions do not necessarily cover the same orders and families and sometimes there are considerable discrepancies. Changes have also been made in the linear sequence, reflecting the development of Thorne's ideas about probable phylogenetic pathways and the relationships of subordinate taxa. The most recent sequence is indicated by numbers in Table 6. Thorne has presented his system not only in a linear sequence, but also in a two-dimensional diagram as a present-day cross-section through an imaginary phylogenetic 'tree', showing the presumed relationships of taxa down to the level of order.

Of the orders recognised by Thorne, 51 are represented in Australia by native species. This is the lowest number for all seven authors discussed here and only about half that of Hutchinson (Table 5). It is, however, only slightly less than that of Melchior and, like the latter, Thorne emphasises the rank of suborder. He recognises a total of 86 suborders and undivided orders indigenous in the region, comparable with the numbers of orders in Dahlgren and Takhtajan. The following of Cronquist's orders are ranked by Thorne as suborders: *Aristolochiales*, *Laurales*, *Piperales* (in *Annonales*), *Dilleniales*, *Lecythidales*, *Nepenthales* (in *Theales*), *Fabales*, *Sapindales* (in *Rutales*), *Haloragales*, *Rhizophorales* (in *Cornales*), *Linales*, *Polygalales* (in *Geraniales*), *Plumbaginales* (in *Primulales*); *Eriocaulales*, *Juncales* (in *Commelinales*), and *Orchidales* (in *Liliales*). Some of Cronquist's smaller orders are accepted by Thorne only at family level, viz. *Batales* (in *Rutales*), *Callitrichales* (in *Lamiales*), *Plantaginales* (in *Bignoniales*), *Podostemales* (in *Rosales*), *Rubiales* (in *Gentianales*); *Cyperales*, *Restionales* (in *Commelinales*), *Hydatellales* (*familia incertae sedis*) and *Hydrocharitales* (in *Alismatales*). By contrast, seven orders are recognised by Thorne (and others) but not by Cronquist (Table 7). Three of these have been recognised recently, viz. *Balanophorales*, *Boraginales* and *Nelumbonales*, whereas *Oleales* has been transferred from *Santaliflorae* to *Gentianiflorae*. Unusual names are *Annonales* (for *Magnoliales s. lat.*), *Berberidales* (for *Ranunculales*), *Bignoniales* (for *Scrophulariales s. lat.*) and *Chenopodiales* (for *Caryophyllales*).

Table 7. An alphabetical list of all orders of Flowering Plants in Australia. Alternative positions for segregate orders in (usually) larger ones are indicated by indented names, some highlighted (!).

Hutchinson (1973)	**Dahlgren (1980)**	**Takhtajan (1980)**	**Cronquist (1981)**	**Melchior (1964)**	**Thorne (1981)**
Agavales	Asparagales	Liliales	Liliales	Liliiflorae	Liliales
Alismatales	Alismatales	Alismatales	Alismatales	Helobiae	Alismatales
Alstroemeridales	Asparagales(!)	Smilacales(!)	Liliales	Liliiflorae	Liliales
Amaryllidales	Asparagales(!)	Liliales	Liliales	Liliiflorae	Liliales
Annonales	Annonales	Magnoliales	Magnoliales	Magnoliales	Annonales (incl. Magnoliineae)
(Apiales) =Umbellales	Araliales	Araliales	Apiales	Umbelliflorae	Araliales
Apocynales	Gentianales	Gentianales	Gentianales	Gentianales	Gentianales
Aponogetonales	Hydrocharitales	Najadales	Najadales	Helobieae	Zosterales
Arales	Arales	Arales	Arales	=Spathiflorae	Arales
Araliales	Araliales	Araliales	Apiales	=Umbelliflorae	Araliales
=Palmales	Arecales	Arecales	Arecales	=Principes	Arecales
Aristolochiales	Aristolochiales	Aristolochiales	Aristolochiales	Aristolochiales	Annonales
Liliales	Asparagales(!)	Liliales	Liliales	Liliiflorae	Liliales
Asterales	Asterales	Asterales	Asterales	Campanulales	Asterales
Balanopsidales	Balanopales	Balanopales	Fagales(!)	Balanopales	Pittosporales
Santales	Balanophorales	Balanophorales	Santales(!)	Balanophorales	Balanophorales
Chenopodiales	Capparales(!)	Sapindales	Batales	Batales	Rutales
Cucurbitales	Violales	Begoniales	Violales	Violales	Violales
Berberidales	Ranunculales	Ranunculales	Ranunculales	Ranunculales	Berberidales *s. lat.*
Bignoniales	Scrophulariales	Scrophulariales	Scrophulariales	Tubiflorae	Bignoniales *s. lat.*
Bixales	Malvales	Violales	Violales	Violales	Malvales
Boraginales	Boraginales	Polemoniales(!)	Lamiales(!)	Tubiflorae	Boraginales
Brassicales	Capparales	Capparales	Capparales	Papavarales	Capparales
Burmanniales	Burmanniales	Burmanniales	Orchidales(!)	Liliiflorae	Liliales
Butomales	Alismatales	Alismatales	Alismatales	Helobiae	Alismatales
Onagrales	Lamiales	Lamiales	Callitrichales	Tubiflorae	Lamiales
Campanales	Campanulales	Campanulales	Campanulales	Campanulales	Campanulales
Capparales	Capparales	Capparales	Capparales	=Papaverales	Capparales
Caryophyllales	Caryophyllales	Caryophyllales	Caryophyllales	=Centrospermae	=Chenopodiales
Casuarinales	Casuarinales	Casuarinales	Casuarinales	Casuarinales	Casuarinales

Celastrales	Celastrales	Celastrales	Celastrales	Celastrales	Celastrales
Chenopodiales	Caryophyllales	Caryophyllales	Caryophyllales	Centrospermae	Chenopodiales *s. lat.*
(Clusiales) =Guttiferales	Theales	Theales	Theales	Guttiferales *s. lat.*	Theales
Commelinales	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
Dilleniales	Sapindales	Connarales	Sapindales	Rosales	Rutales
Araliales	Cornales	Cornales	Cornales	Umbelliflorae	Cornales
Cucurbitales	Violales	Violales	Violales	Cucurbitales	Violales
Cunoniales	Cunoniales	Saxifragales	Rosales	Rosales	Rosales
Cyperales	Cyperales	Cyperales	Cyperales	Cyperales	Commelinales
Dilleniales	Dilleniales	Dilleniales	Dilleniales	Guttiferales	Theales
Dioscoreales	Dioscoreales	Smilacales	Liliales	Liliiflorae	Liliales
Araliales	Cornales	Dipsacales	Dipsacales	Dipsacales	Dipsacales
Sarraceniales	Droserales	Saxifragales	Nepenthales(!)	Sarraceniales	Rosales
Ebenales	Ebenales	Ebenales	Ebenales	Ebenales	Ebenales
Rhamnales	Elaeagnales	Elaeagnales	Proteales(!)	Thymelaeales	Rhamnales
Ericales	Ericales	Ericales	Ericales	Ericales	Ericales
Eriocaulales	Eriocaulales	Eriocaulales	Eriocaulales	Commelinales	Commelinales
Euphorbiales	Euphorbiales	Euphorbiales	Euphorbiales	Geraniales	Euphorbiales
=Leguminales	Fabales	Fabales	Fabales	Rosales	Rutales
Fagales	Fagales	Fagales	Fagales	Fagales	Fagales
Gentianales	Gentianales	Gentianales	Gentianales	Gentianales	Gentianales
Geraniales	Geraniales	Geraniales	Geraniales	Geraniales	Geraniales
Goodeniales	Goodeniales	Campanulales	Campanulales	Campanulales	Campanulales
Onagrales	Gunnerales	Saxifragales(!)	Haloragales(!)	Myrtiflorae	Cornales
Haemodorales	Haemodorales	Liliales	Liliales	Liliiflorae	Liliales
Onagrales	Haloragales	Myrtales(!)	Haloragales	Myrtiflorae	Cornales
Hamamelidales	Hamamelidales	Hamamelidales	Hamamelidales	Rosales	Hamamelidales
Juncales	Hydatellales	Hydatellales	Hydatellales	Commelinales	Hydatellaceae (*stat. dub.*)
Butomales	Hydrocharitales	Alismatales	Hydrocharitales	Helobiae	Alismatales
Iridales	Liliales	Liliales	Liliales	Liliiflorae	Liliales
Juncaginales	Zosterales	Najadales	Najadales	Helobiae	Zosterales
Juncales	Juncales	Juncales	Juncales	Juncales	Commelinales
Lamiales	Lamiales	Lamiales	Lamiales	Tubiflorae	Lamiales
Laurales	Laurales	Laurales	Laurales	Magnoliales	Annonales
Myrtales	Theales	Myrtales	Lecythidales	Myrtiflorae	Theales

Table 7 (cont.)

Hutchinson (1973)	**Dahlgren (1980)**	**Takhtajan (1980)**	**Cronquist (1981)**	**Melchior (1964)**	**Thorne (1981)**
Liliales	Liliales	Liliales	Liliales	=Liliiflorae	Liliales
Malphigiales	Geraniales	Geraniales	Linales	Geraniales	Geraniales
Loganiales	Gentianales	Gentianales	Gentianales	Gentianales	Gentianales
Magnoliales	Magnoliales	Magnoliales	Magnoliales	Magnoliales	Annonales
Malpigiales (see also Linales)	Polygalales	Polygalales	Polygalales	Rutales	Geraniales
Malvales	Malvales	Malvales	Malvales	Malvales	Malvales
Meliales	Rutales	Rutales	Sapindales(!)	Rutales	Rutales
Myrsinales	Primulales	Primulales	Primulales	Primulales	Primulales
Myrtales	Myrtales	Myrtales	Myrtales	=Myrtiflorae	Myrtales
Najadales	Zosterales	Najadales	Najadales	=Helobiae *p.p. maj.*	Najadales
Ranales	Nelumbonales	Nelumbonales	Nymphaeales	Ranunculales	Nelumbonales
Aristolochiales	Theales	Nepenthales	Nepenthales	Sarraceniales	Theales
Ranales	Nymphaeales	Nymphaeales	Nymphaeales	Ranunculales	Nymphaeales
Ochnales	Theales	Theales	Theales	Guttiferales	Theales
Olacales	Santalales	Santalales	Santalales	Santalales	Santalales
Loganiales	Oleales	Oleales	Scrophulariales(!)	Oleales	Oleales
Onagrales	Myrtales	Myrtales	Myrtales	Myrtiflorae	Myrtales
Orchidales	Orchidales	Orchidales	Orchidales	=Microspermae	Liliales
Pandanales	Pandanales	Pandanales	Pandanales	Pandanales	Pandanales
Passiflorales	Violales	Violales	Violales	Violales	Violales
Haemodorales	Phylidrales	Liliales	Liliales	Liliiflorae	Commelinales
Piperales	Piperales	Piperales	Piperales	Piperales	Annonales
Pittosporales	Pittosporales	Saxifragales	Rosales	Rosales	Pittosporales
Plantaginales	Scrophulariales	Scrophulariales	Plantaginales	Plantaginales	Bignoniales
Primulales	Plumbaginales	Plumbaginales	Plumbaginales	Plumbaginales	Primulales
=Graminales	Poales	Poales	Cyperales(!)	=Graminales	Commelinales
Podostemales	Podostemales	Podostemales	Podostemales	Podostemales	Rosales
Polemoniales	Solanales	Polemoniales	Solanales	Tubiflorae	Solanales
Polygalales	Polygalales	Polygalales	Polygalales	Rutales	Geraniales
Polygonales	Polygonales	Polygonales	Polygonales	Polygonales	Polygonales
Liliales	Pontederiales	Liliales	Liliales	Liliiflorae	Commelinales

Potamogetonales	Zosterales(!)	Najadales	Najadales	Helobiae	Zosterales
Primulales	Primulales	Primulales	Primulales	Primulales	Primulales
Proteales	Proteales	Proteales	Proteales	Proteales	Proteales
Aristolochiales	Rafflesiales	Rafflesiales	Rafflesiales	Aristolochiales	Rafflesiales
Ranales	Ranunculales	Ranunculales	Ranunculales	Ranunculales	=Berberidales
Juncales	Poales	Restionales	Restionales	Commelinales	Commelinales
Rhamnales	Rhamnales	Rhamnales	Rhamnales	Rhamnales	Rhamnales
Myrtales	Rhizophorales	Myrtales	Rhizophorales	Myrtiflorae	Cornales
Rosales	Rosales	Rosales	Rosales	Rosales	Rosales
Rubiales	Gentianales	Gentianales	Rubiales	Gentianales	Gentianales
Rutales	Rutales	Rutales	Sapindales(!)	Rutales	Rutales
Santalales	Santalales	Santalales	Santalales	Santalales	Santalales
Sapindales	Sapindales	Sapindales	Sapindales	Sapindales	Rutales
Sarraceniales	Droserales	Saxifragales	Nepenthales	Sarraceniales	Rosales
Saxifragales	Saxifragales	Saxifragales	Rosales	Rosales	Rosales
=Personales	Scrophulariales	Scrophulariales	Scrophulariales	=Tubiflorae *p.p. maj.*	=Bignoniales
Liliales	Asparagales(!)	Smilacales	Liliales	Liliales	Liliales
Solanales	Solanales	Scrophulariales(!)	Solanales	Tubiflorae	Solanales
Styracales	Cornales(!)	Ebenales	Ebenales	Ebenales	Theales
Tamaricales	Tamaricales	Tamaricales	Violales	Violales	Violales
Theales	Theales	Theales	Theales	=Guttiferales	Theales
Thymelaeales	Thymelaeales	Thymelaeales	Myrtales(!)	Thymelaeales	Euphorbiales
Tiliales	Malvales	Malvales	Malvales	Malvales	Malvales
Triuridales	Triuridales	Triuridales	Triuridales	Triuridales	Triuridales
Typhales	Typhales	Typhales	Typhales	Pandanales	Typhales
Urticales	Urticales	Urticales	Urticales	Urticales	Urticales
Verbenales	Lamiales	Lamiales	Lamiales	Tubiflorae	Lamiales
Violales	Violales	Violales	Violales	Violales	Violales
Rhamnales	Vitidales	Rhamnales	Rhamnales	Rhamnales	Cornales
Xyridales	Eriocaulales	Commelinales	Commelinales	Commelinales	Commelinales
Zingiberales	Zingiberales	Zingiberales	Zingiberales	=Scitamineae	Zingiberales
Aponogetonales	Zosterales	Najadales	Najadales	Helobiae	Zosterales

Of the taxa ranked as orders by Takhtajan, but not by Cronquist or Thorne, the following are ranked as suborders by Thorne: *Balanopales* (newly in *Pittosporales*), *Begoniales* (in *Violales*), *Polemoniales* (in *Solanales*), *Saxifragales* (in *Rosales*), *Tamaricales* (newly in *Violales*); *Poales* (in *Commelinales*). Also, the following of Takhtajan's orders are recognised by Thorne only as families: *Connarales* (newly in *Rutales*, transferred from *Rosales*), *Elaeagnales* (in *Rhamnales*), *Thymelaeales* (in *Euphorbiales*); *Burmanniales* (in *Liliales*) and *Smilacales* (as subfamily in *Liliaceae*). Other changes at the level of order in Thorne's system between 1976 and 1981 not indicated above are the elevation of *Araliales* (from suborder in *Cornales*), *Celastrales* (from suborder in *Santalales*), *Typhales* (from suborder in *Arales*, also as a distinct superorder), and the introduction of the new name *Violales* (for *Cistales*, *Tamaricales* and the introduced *Salicales*).

Thorne recognises only 190 families with indigenous species in Australia, which is the lowest number for all systems discussed here (Table 5). As in the case of his orders, he regards a further subdivision of his families as important. Twenty seven families are accepted by Cronquist but not, or no longer, by Thorne (Table 8). On the other hand, Thorne accepts three families not recognised by Cronquist, viz. *Baueraceae* (next to *Cunoniaceae*, in 1981), *Cochlospermaceae* (next to *Bixaceae*, in 1981) and *Sphenostemonaceae* (new since 1976). Two other differences between the systems of Thorne and Cronquist are Thorne's placing of *Blepharocaryaceae* (in *Anacardiaceae* since 1976, rather than in *Sapindaceae*) and *Stylobasiaceae* (in *Sapindaceae* since 1976, rather than *Surianaceae*). Changes in Thorne's system at family level, not mentioned above, are the relegation of *Gyrocarpaceae* to *Hernandiaceae* (1976), the recognition of *Nelumbonaceae* (out of *Nymphaeaceae*, 1976); *Costaceae* (next to *Zingiberaceae*, 1981), *Cymodoceaceae* (next to *Zanichelliaceae*), *Hydatellaceae* (new in 1981) and the use of the name *Juncaginaceae* in preference to *Scheuchzeriaceae* (since 1976). Finally, Thorne agrees with Cronquist in relegating *Amaryllidaceae* and *Hypoxidaceae* to *Liliaceae*.

R. M. T. Dahlgren's system

Rolf Dahlgren's system is the most recent of those discussed in this chapter and in many ways the most modern. The first version appeared in 1975 followed by a thoroughly revised one in 1980. Dahlgren's approach is probably the most truly 'cladistic', since he has relied more on numerical methods and less on personal intuition. He has aimed for a 'radical' solution, although he certainly has not entirely broken with tradition. Groups that could be distinguished taxonomically were ranked—probably for prominence—as orders or families rather than as subordinate taxa, even though this often led to an otherwise regrettable inflation.

An interesting feature of Dahlgren's system is its presentation in a two-dimensional diagram (Fig. 22), representing a contemporary cross-section through an imaginary phylogenetic 'tree'. The superorders were shaped by the relative size of their constituent orders, and relative distances were based on ratios of similarities and dissimilarities in a number of characters. The principal diagrams of the successive editions were also used as 'base maps' to demonstrate the distribution of various characters throughout the Flowering Plants (e.g. sympetaly, as in Fig. 22).

Dahlgren treated Flowering Plants as a class (*Magnoliopsida*), divided primarily into Dicots (*Magnoliidae*) and Monocots (*Liliidae*), which were ranked as subclasses as in Thorne's system. His next division was into 24 superorders within the Dicots (only one, *Loasiflorae*, not represented in Australia) and 7 within the Monocots. These are comparable with the equivalent numbers in Takhtajan's and Thorne's systems (Tables 5 and 6), although there are major differences between the circumscrip-

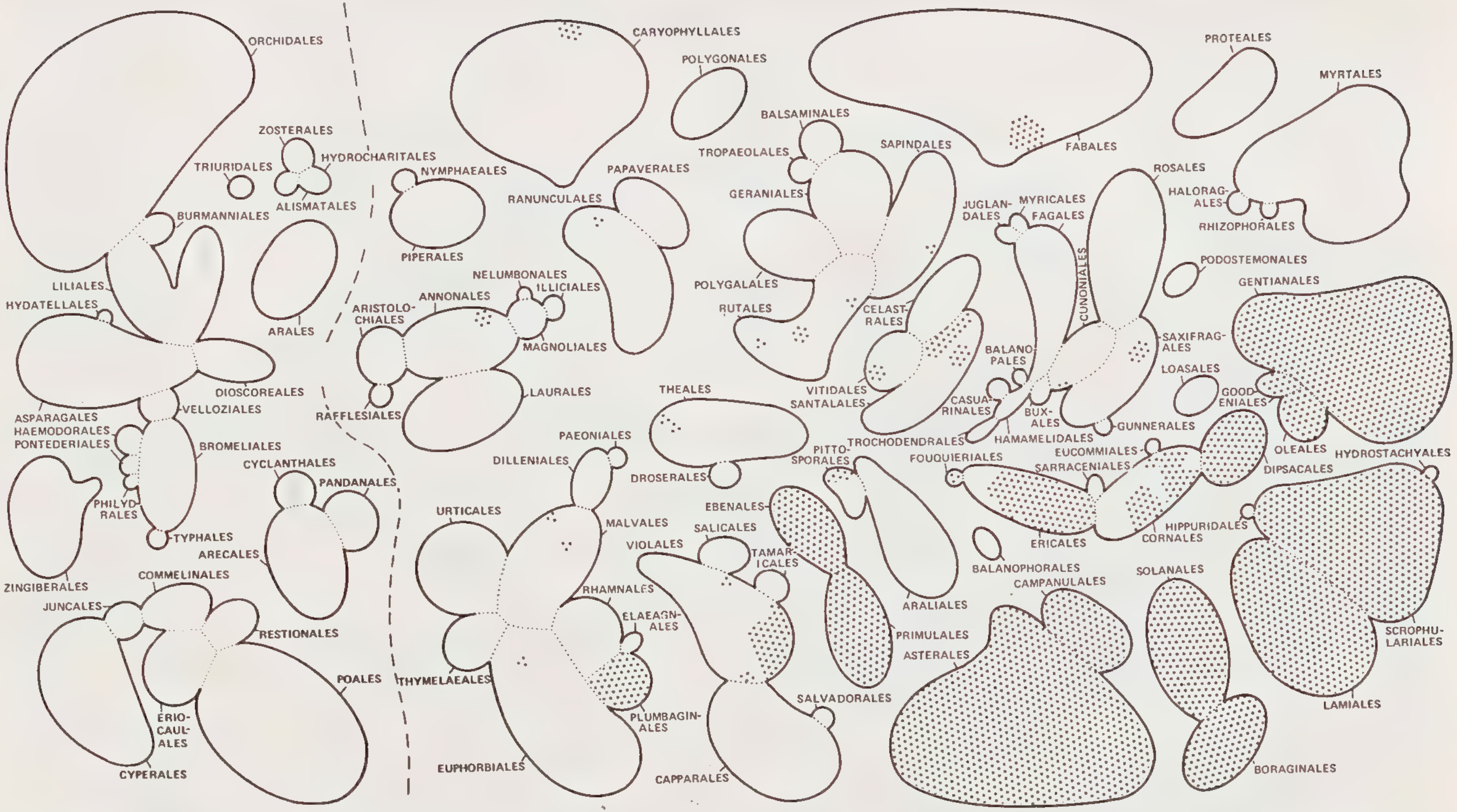

Figure 22. The orders of the *Magnoliophyta* (Flowering Plants), shown as clusters of superorders. The broken line separates the classes *Liliopsida* (Monocotyledons) on the left and *Magnoliopsida* (Dicotyledons) on the right. Shading indicates the occurrence of sympetalous flowers in orders (or parts thereof) of the latter class, showing that taxa similar in this respect may not be closely related. The diagram could be interpreted as a chronological cross-section (the present) through the branching system of an imaginary phylogenetic tree. (After Dahlgren, 1980; reproduced by permission of the author)

tions of taxa by these three authors. In Dahlgren's latest system, the names of the superorders were given the suffix *-florae* (following Thorne, 1968, 1976) rather than the more widely applicable *-anae* of his first edition (in accordance with Takhtajan, 1969, 1980). It also presented additional superorders, viz. *Fabiflorae* (out of *Rosanae*), *Podostemoniflorae* (out of *Saxifraganae*), *Polygoniflorae* (out of *Plumbaginanae*) and *Triuridiflorae* (out of *Lilianae*). Newly synonymised superorders were: *Campanulanae* (in *Asteriflorae*), *Dillenianae*, *Plumbaginanae* p.p. and *Thymelaeanae* (under the new name *Malviflorae*), *Hamamelidanae* and *Saxifraganae* p.p. (in *Rosiflorae*), *Rafflesianae* (in *Magnoliiflorae*) and *Typhanae* (in *Liliiflorae*). The new name *Santaliflorae* covered many of the subordinate taxa of the previous *Celastranae*. Further alterations were proposed in the linear arrangement of the superorders, as well as in the circumsciptions of several similarly named ones.

Of the 105 orders of Flowering Plants recognised by Dahlgren, 84 are represented in Australia by native species: a relatively high number (Table 5). Some 25 of Dahlgren's indigenous orders are not recognised by Cronquist, whereas the latter recognises 10 orders that were not (or no longer) adopted by Dahlgren (Table 7). Like other authors, Dahlgren used the name *Araliales* for Cronquist's *Apiales*. Further, he recognised eight orders for the first time in 1980, viz. *Annonales*, (in *Magnoliiflorae*), *Boraginales* (in *Solaniflorae*), *Rhizophorales* (in *Myrtiflorae*), *Vitidales* (in *Santaliflorae*); *Hydatellales*, *Phylidrales*, *Pontederiales* (all in *Liliiflorae*) and *Zosterales* (in *Alismatiflorae*). Similarly, five orders were synonymised viz. *Nepenthales* (in *Theales*); *Centrolepidales* (in *Poales*), *Najadales* (in *Zosterales*), *Stemonales* and *Taccales* (both in *Dioscoreales*).

In the latest edition of his system (1980), Dahlgren recognised 234 families with indigenous representatives in Australia, the second highest number of the six systems discussed here, not far behind Airy Shaw's total. He accepted segregate families when there was doubt about the correct placement of the genera concerned, but changes in the second edition make it clear that he was content to synonymise such families once a more satisfactory position had been found. Thirty three families were recognised by Dahlgren but not by Cronquist (Table 8). Apart from the changes mentioned above, the following families were newly recognised by Dahlgren in 1980: *Corokiaceae* (in *Cornales*), *Sonneratiaceae* (in *Myrtales*), *Thunbergiaceae* (in *Scrophulariales*), *Asteliaceae*, *Dasypogonaceae*, *Dianellaceae*, *Doryanthaceae nom. nud.*, *Geitonoplesiaceae nom. nud.*, *Hanguanaceae*, *Luzuriagaceae* and *Petermanniaceae* (all in *Asparagales*) and *Hydatellaceae* (in *Hydatellales*?). The following were synonymised in 1980: *Dysphaniaceae* (in *Chenopodiaceae*), *Gyrocarpaceae* (in *Hernandiaceae*), *Idiospermaceae* (in *Calycanthaceae*), *Leeaceae* (in *Vitaceae*), *Orobanchaceae* (in *Scrophulariaceae*), *Potaliaceae*, *Spigeliaceae* and *Strychnaceae* (in *Loganiaceae*), *Siphonodontaceae* (in *Celastraceae*), *Sphenocleaceae* (in *Campanulaceae*), *Stylobasiaceae* (in *Sapindaceae*), *Xanthophyllaceae* (in *Commelinaceae*), *Ecdeiocoleaceae* (in *Restionaceae*) and *Limnocharitaceae* (in *Alismataceae*). Finally, in 1980 Dahlgren introduced *Hypericaceae* for *Clusiaceae* as used in 1975.

Concluding remarks

After the preceding discussions of seven authors and six systems, the following general remarks can be made:

1. The Flowering Plants still are subdivided primarily into Monocots and Dicots, although modern authors appear to be increasingly dissatisfied with these two as equivalent natural groups, the former taxon probably being regarded as the more homogeneous (see e.g. Dahlgren, 1980).

2. The traditional further subdivisions above the level of order, based on one or a few

related characters, have practically disappeared since Melchior's (1964). An original division into subclasses was developed by Cronquist and largely adopted by Takhtajan (Table 6). Thorne and Dahlgren only recognise Monocots and Dicots at that rank. Hutchinson's comparable 'Divisions' have generally been rejected as being too artificial. A division into superorders has been pioneered and developed by Takhtajan, whereas Thorne and Dahlgren have adopted similar approaches.

3. There is still a controversy between the 'conservatives' such as Thorne (and previously Melchior) and the 'radicals' such as Dahlgren (previously also Hutchinson and Airy Shaw) about the assignment of taxa to certain ranks. The former prefers the ranks of suborder and subfamily to indicate 'lesser' taxonomic differences, whereas the latter gives greater exposure to any relevant distinctions at the major ranks of order and family. Cronquist and Takhtajan occupy positions in the middle of this spectrum, although the latter—in other ways slightly more 'radical'—makes a more consistent use of all ranks available for subdivision (Table 5).

4. Dahlgren (1975a, 1980) and Thorne (1976, 1981) have produced a superior type of two-dimensional diagram, presented as a horizontal cross-section through an imaginary phylogenetic 'tree', to illustrate their systems of the recent Flowering Plants. Diagrams of a traditional format, looking more or less like vertical 'genealogical trees' of exclusively recent taxa (e.g. Hutchinson 1973, Takhtajan 1969), are open to misinterpretations of a pseudo-phylogenetic nature and should therefore be discouraged. The latter type is only acceptable if all recent taxa are placed at the tips of the branches, i.e. only allowing for a one-dimensional arrangement of these. It should be remembered, however, that even a two-dimensional diagram is less than ideal as a means to express relationships which are actually multi-dimensional in nature. Although Dahlgren in particular has reached a new level of sophistication (Fig. 22), it should be pointed out that some of his principles were previously applied by A. A. Pulle (1952), whose diagram—with circles of various sizes representing orders and some of their character-states—was reproduced by Melchior (1964).

5. A recent trend is the recognition by several authors of a greater or smaller number of segregate families (and orders) in the *Rosiflorae* (and the transfer of some of these taxa to *Araliiflorae* and *Corniflorae* by Dahlgren). Another tendency is the recognition of an increasing number of orders and families in the *Liliiflorae* by Takhtajan and particularly Dahlgren (as well as a large number of subfamilies by Thorne). Both developments were strongly influenced by the studies of Huber (1963, 1969). Further concepts subject to radical change are, e.g., those of *Violiflorae / Malviflorae* and *Rutiflorae / Geraniiflorae*, whereas the placing of several individual orders and families is equally not yet resolved to everyone's satisfaction. Although there is certainly much common ground between the four most recent authors discussed here, there are also diverging developments in their ideas about a number of groups and a consensus, even in general terms, is still some time off.

References

The following list provides not only more complete citation of references given in the text, but also a selection of additional books and papers relevant to Flowering Plant Taxonomy (asterisked *). Preference has been given to contributions of the last ten to fifteen years, although some older but still relevant ones have been included. Published proceedings of symposia have been listed under their general titles; some papers have been listed individually under the relevant author.

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Table 8. Families of Flowering Plants with taxa indigenous in Australia as recognised by four authors, but not regarded as distinct at that level by all four. Alternative taxonomic positions of segregate families indicated by indented names, some queried (?), some highlighted (!).

R.M.T. Dahlgren (1980)	**A. Takhtajan (1980)**	**A. Cronquist (1981)**	**R.F. Thorne (1981)**
Aegicerataceae Blume	Myrsinaceae	Myrsinaceae	Myrsinaceae—Myrsinoideae
Agavaceae Endl.	Agavaceae	Agavaceae	Liliaceae—Agavoideae
Amaryllidaceae J. St.Hil.	Amaryllidaceae	Liliaceae	Liliaceae—Amaryllidoideae
Anthericaceae J. Agardh	Asphodelaceae(?)	Liliaceae	Liliaceae—Asphodeloideae(?)
Apiaceae Lindley	Apiaceae	Apiaceae	Araliaceae—Apioideae
Apostasiaceae Lindley	Orchidaceae	Orchidaceae	Orchidaceae—Apostasioideae
Asclepiadaceae R. Br.	Asclepiadaceae	Asclepiadaceae	Apocynaceae—Asclepiadoideae
Asparagaceae A.L. Juss.	Asparagaceae	Liliaceae	Liliaceae—Asparagoideae
Asphodelaceae A.L. Juss.	Asphodelaceae	Liliaceae	Liliaceae—Asphodeloideae
Asteliaceae Dumort.	Dracaenaceae	Agavaceae	Liliaceae—Dracaenoideae(?)
Baueraceae Lindley	Cunoniaceae	Cunoniaceae	Baueraceae
Goodeniaceae	Goodeniaceae	Brunoniaceae DC.	Goodeniaceae—Brunonioideae
Caesalpiniaceae R. Br.	Fabaceae	Caesalpiniaceae	Fabaceae—Caesalpinioideae
Cochlospermaceae Planchon	Bixaceae	Bixaceae	Cochlospermaceae
Colchicaceae DC.	Colchicaceae	Liliaceae	Liliaceae—Wurmbaeoideae(?)
Corokiaceae *nom. nud.*	Escalloniaceae	Saxifragaceae	Saxifragaceae—Escallonioideae
Corsiaceae Becc.	Corsiaceae	Corsiaceae	Burmanniaceae—Corsioideae
Cuscutaceae Dumort.	Cuscutaceae	Cuscutaceae	Convolvulaceae—Cuscutoideae
Dasypogonaceae Dumort.	Xanthorrhoeaceae	Xanthorrhoeaceae	Linaceae—Xanthorrhoeoideae
Dianellaceae Salisb.	Phormiaceae	Liliaceae	Liliaceae—Agavoideae(?)
Stylidiaceae	Stylidiaceae	Donatiaceae Dostál	Stylidiaceae—Donatioideae
Doryanthaceae *nom. nud.*	Doryanthaceae	Agavaceae	Liliaceae—Agavoideae
Dracaenaceae Salisb.	Dracaenaceae	Agavaceae	Liliaceae—Dracaenoideae
Restionaceae	Ecdeiocoleaceae D. Cutler & Airy Shaw	Restionaceae	Restionaceae—Ecdeiocoleoideae
Ehretiaceae Lindley	Boraginaceae	Boraginaceae	Boraginaceae—Ehretioideae
Emblingiaceae Airy Shaw	Emblingiaceae	Polygalaceae(!)	Capparaceae—(?)
Eremosynaceae Takht.	Eremosynaceae	Saxifragaceae	Saxifragaceae—Eremosynoideae
Escalloniaceae Dumort.	Escalloniaceae	Grossulariaceae(!)	Saxifragaceae—Escallonioideae
Geitonoplesiaceae *nom. nud.*	Philesiaceae	Smilacaceae	Liliaceae—Luzuriagoideae(?)
Haemodoraceae R. Br.	Haemodoraceae	Haemodoraceae	Liliaceae—Haemodoroideae

Hanguanaceae Airy Shaw	Hanguanaceae	Hanguanaceae	Liliaceae—Xanthorrhoeoideae
Celastraceae	Celastraceae	Hippocrateaceae A.L. Juss.	Celastraceae—Hippocrateoideae
Hypericaceae A.L. Juss. (incl. Clusiaceae)	Clusiaceae	Clusiaceae	Clusiaceae
Hypoxidaceae R. Br.	Hypoxidaceae	Liliaceae	Liliaceae—Hypoxidoideae
Calycanthaceae	Calycanthaceae	Idiospermaceae S.T. Blake	Calycanthaceae—Idiospermoideae
Vitaceae	Leeaceae Dumort.	Leeaceae	Vitaceae—Leeoideae
Alismataceae	Limnocharitaceae Takht.	Limnocharitaceae	Alismataceae—Limnocharitoideae
Limoniaceae Lincz.	Plumbaginaceae	Plumbaginaceae	Plumbaginaceae—Staticoideae(?)
Lobeliaceae R. Br.	Campanulaceae	Campanulaceae	Campanulaceae—Lobelioideae
Luzuriagaceae Dostál	Philesiaceae	Smilacaceae	Liliaceae—Luzuriagoideae
Mimosaceae R. Br.	Fabaceae	Mimosaceae	Fabaceae—Mimosoideae
Molluginaceae Hutch.	Molluginaceae	Molluginaceae	Aizoaceae—Molluginoideae
Moraceae Link	Moraceae	Moraceae	Urticaceae—Moroideae
Nitrariaceae Lindley	Nitrariaceae	Zygophyllaceae	Zygophyllaceae—Nitrarioideae
Opiliaceae Valeton	Opiliaceae	Opiliaceae	Olacaceae—Opilioideae
Scrophulariaceae	Orobanchaceae Vent.	Orobanchaceae	Scrophulariaceae—Orobanchoideae
Petermanniaceae Hutch.	Philesiaceae	Smilacaceae	Liliaceae—Luzuriagoideae(?)
Philesiaceae Dumort.	Philesiaceae	Smilacaceae	Liliaceae—Luzuriagoideae(?)
Phormiaceae J. Agardh	Phormiaceae	Agavaceae	Liliaceae—Agavoideae
Potamogetonaceae	Ruppiaceae Hutch.	Ruppiaceae	Potamogetonaceae
Sambucaceae Link	Caprifoliaceae(?)	Caprifoliaceae	Caprifoliaceae—Sambucoideae
Celastraceae	Siphonodontaceae Tard.	Celastraceae	Celastraceae—Siphonodontoideae
Smilacaceae Vent.	Smilacaceae	Smilacaceae	Liliaceae—Smilacoideae
Sonneratiaceae Engl. & Gilg	Sonneratiaceae	Sonneratiaceae	Lythraceae—Sonneratioideae
Sparganiaceae Rudolphi	Typhaceae	Sparganiaceae	Typhaceae—Sparganioideae
Campanulaceae	Campanulaceae	Sphenocleaceae DC.	Campanulaceae—Sphenocleoideae
Sphenostemonaceae P. Royen & Airy Shaw	Sphenostemonaceae	Aquifoliaceae(?)	Sphenostemonaceae
Sapindaceae	Stylobasiaceae J. Agardh	Surianaceae(!)	Sapindaceae—Stylobasioideae
Surianaceae Arn.	Simaroubaceae	Surianaceae	Surianaceae
Tetracarpaeaceae Nakai	Escalloniaceae	Saxifragaceae	Saxifragaceae—Tetracarpaeoideae
Thismiaceae J. Agardh	Burmanniaceae	Burmanniaceae	Burmanniaceae—Thismioideae
Thunbergiaceae Tieghem	Acanthaceae	Acanthaceae	Acanthaceae—Thunbergioideae
Polygalaceae	Polygalaceae	Xanthophyllaceae Gagnep.	Polygalaceae
Xanthorrhoeaceae Dumort.	Xanthorrhoeaceae	Xanthorrhoeaceae	Liliaceae—Xanthorrhoeoideae

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Opposite. Spring flora on a granitic slope of the Darling Scarp east of Perth, Western Australia, with Eucalypt woodland on the skyline. Photograph — A. S. George

Overleaf. Open forest of *Eucalyptus nitens* (Deane & Maiden) Maiden, near Bendoc, East Gippsland, Victoria. Photograph — R. D. Johnston

KEY TO FAMILIES OF FLOWERING PLANTS

H. T. Clifford

1	Embryo with 1 cotyledon; leaf venation usually convergent; leaf base usually sheathing; perianth 3– (occasionally 2– or 4–) merous (monocotyledons)	838
	Embryo with 2 (rarely 1, 3 or more) cotyledons; leaf venation usually reticulate; leaf base rarely sheathing; perianth 4–5– (rarely 3– or more than 5–) merous (dicotyledons)	2

Dicotyledons

2	Flowers with at least one perianth whorl	3
	Flowers lacking perianth	820
3	Either one or both perianth whorls fused into a cap	4
	Perianth segments not fused into a cap	10
4	Leaves invested with peltate scales	**Himantandraceae**
	Leaves glabrous or, if indumentum present, not of peltate scales	5
5	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	6
6	Leaf base sheathing	**Epacridaceae**
	Leaf base not sheathing	7
7	Leaves exstipulate	**Eupomatiaceae**
	Leaves stipulate	8
8	Tendrils present	**Vitaceae**
	Tendrils absent	9
9	Gynophore present; leaves usually alternate	**Capparaceae**
	Gynophore absent; leaves opposite	**Eucryphiaceae**
10	Perianth segments more than 6 (counting sepals and petals if both present)	11
	Perianth segments 6 or fewer (counting sepals and petals if both present but not barks, scales or plumes on fruit)	572
11	Corolla segments (or perianth segments) free	12
	Corolla segments (or perianth segments) united	386
12	All or most flowers unisexual	13
	Most flowers bisexual	44
13	Ovary superior	14
	Ovary inferior	40

14	Floating aquatics; leaves whorled, much divided	**Ceratophyllaceae**
	Land plants; leaves alternate, opposite, or absent	**15**
15	Gynoecium apocarpous	**16**
	Gynoecium syncarpous or carpel 1	**18**
16	(1) Climbers; leaves opposite	**Rutaceae**
	(2) Climbers (or plants spreading over the ground); leaves alternate	**Menispermaceae**
	(3) Non-climbers, not spreading	**17**
17	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**Simaroubaceae**
18	Leaves compound	**19**
	Leaves simple or absent	**25**
19	Petals 4	**20**
	Petals 5	**22**
20	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**21**
21	Stamens 3–5 in male flowers	**Simaroubaceae**
	Stamens usually 8 in male flowers	**Anacardiaceae**
22	Stamens 5 in male flowers	**Anacardiaceae**
	Stamens more than 5 in male flowers	**23**
23	Stamens usually 8; style 1; stigma entire or lobed	**Sapindaceae**
	Stamens 10; styles or stigmas more than 1	**24**
24	Ovary entire; stigmas glabrous	**Anacardiaceae**
	Ovary lobed; stigmas plumose	**Simaroubaceae**
25	Leaves opposite	**26**
	Leaves alternate, clustered, or absent	**27**
26	Flowers strictly unisexual; shrubs or trees	**Euphorbiaceae**
	Flowers polygamous; trees usually with yellow sap	**Clusiaceae**
27	Climbers with tendrils	**Passifloraceae**
	Tendrils absent	**28**
28	Twiners or lianes	**29**
	Shrubs, trees or herbs, sometimes scrambling	**30**
29	Stipules absent; disc absent; petals smaller than sepals, entire, sometimes absent	**Menispermaceae**
	Stipules present; disc present; petals as long as or longer than sepals, emarginate	**Dichapetalaceae**
30	Latex present	**Euphorbiaceae**
	Latex absent	**31**
31	(1) Styles 3, distinct, simple or branched	**Euphorbiaceae**
	(2) Style 1 with 2 or more stigmas	**32**
	(3) Style and stigma 1 or stigma sessile	**35**

32	Male flowers with staminodes	**Tiliaceae**
	Male flowers without staminodes	**33**
33	Ovary 1–locular	**Flacourtiaceae**
	Ovary more than 1–locular	**34**
34	(1) Seeds endospermic; carpels dry, falling entire; leaves not succulent though often thick	**Malvaceae**
	(2) Seeds endospermic; carpels dry, dehiscent; leaves not succulent	**Euphorbiaceae**
	(3) Seeds non-endospermic; fruit a succulent drupe; leaves succulent	**Zygophyllaceae**
35	Calyx segments free	**Euphorbiaceae**
	Calyx segments united or calyx minute	**36**
36	Ovary 1–locular	**37**
	Ovary more than 1–locular	**39**
37	Ovary stipitate	**Capparaceae**
	Ovary sessile	**38**
38	Leaves stipulate	**Malvaceae**
	Leaves exstipulate	**Icacinaceae**
39	Seeds endospermic; leaves not succulent	**Aquifoliaceae**
	Seeds non-endospermic; leaves succulent	**Zygophyllaceae**
40	*(from 13)*	
	Climber with tendrils	**Cucurbitaceae**
	Non-climbers	**41**
41	Herbs or undershrubs	**42**
	Trees	**43**
42	Petals 5	**Apiaceae**
	Petals 0, 2 or 4	**Haloragaceae**
43	Style 1	**Hernandiaceae**
	Styles two or more	**Datiscaceae**
44	*(from 12)*	
	Gynoecium apocarpous	**45**
	Gynoecium syncarpous or carpel 1	**79**
45	Flowers perigynous	**46**
	Flowers hypogynous	**49**
46	Leaves alternate or radical	**47**
	Leaves opposite	**48**
47	Sepals 5; stamens indefinite	**Rosaceae**
	Sepals 4; stamens 4 or 8	**Crassulaceae**
48	Perianth segments indefinite; carpels indefinite	**Idiospermaceae**
	Sepals 4–5; petals 4–5; carpels 4	**Crassulaceae**
49	Stamens indefinite	**50**
	Stamens 10 or fewer	**58**

50	Leaves peltate	**51**
	Leaves not peltate	**52**
51	Carpels embedded in receptacle	**Nelumbonaceae**
	Carpels not embedded in receptacle	**Cabombaceae**
52	Style 1 with 3–5 stigmas	**Ochnaceae**
	Styles (or stigmas when styles much reduced) as many as carpels	**53**
53	Climbers	**54**
	Non-climbers	**55**
54	(1) Perianth segments 10–14	**Austrobaileyaceae**
	(2) Sepals 3; petals 6	**Annonaceae**
	(3) Sepals 4–5; petals 3–5	**Dilleniaceae**
55	(1) Perianth segments all petaloid; herbs	**Ranunculaceae**
	(2) Perianth segments all petaloid; shrubs or trees	**Magnoliaceae**
	(3) One or more whorls of perianth sepaloid	**56**
56	(1) Perianth spiral; leaves with peltate indumentum	**Himantandraceae**
	(2) Perianth 3 + 3 + 3; indumentum, if present, not peltate	**Annonaceae**
	(3) Sepals 5; petals 5; indumentum, if present, not peltate	**57**
57	(1) Herbs; leaves usually much incised	**Ranunculaceae**
	(2) Trees, shrubs, or undershrubs; leaves entire to distinctly incised	**Dilleniaceae**
	(3) Trees; leaves bipinnate	**Mimosaceae**
58	*(from 49)*	
	Style 1, stigmas 1 or more	**59**
	Styles (or stigmas when styles much reduced) free from one another, as many as there are carpels	**64**
59	Leaves peltate	**Tropaeolaceae**
	Leaves not peltate	**60**
60	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**61**
61	Leaves alternate	**62**
	Leaves opposite	**63**
62	Stigma simple	**Ochnaceae**
	Stigmas 3 or more	**Simaroubaceae**
63	Flowers 4–merous	**Rutaceae**
	Flowers 5–merous	**Malpighiaceae**
64	Leaves compound	**65**
	Leaves simple or absent	**66**
65	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**Simaroubaceae**

66	Leaves opposite	**67**
	Leaves alternate, radical, clustered, or absent	**69**
67	Sepals 4; petals 4	**Crassulaceae**
	Sepals 5; petals 5	**68**
68	Petals sessile or with short claws; leaves fleshy	**Crassulaceae**
	Petals with long claws; leaves not fleshy	**Malpighiaceae**
69	(1) Flowers 3–merous (usually sepals 6, petals 6, carpels 6 or 3)	**Menispermaceae**
	(2) Flowers 4–merous	**70**
	(3) Flowers 5–merous	**71**
70	Leaves fleshy; seeds lacking endosperm	**Crassulaceae**
	Leaves not fleshy; seeds endospermic	**Saxifragaceae**
71	Stamens united into one or more groups	**72**
	Stamens free	**73**
72	Carpels 2	**Dilleniaceae**
	Carpels 3	**Malpighiaceae**
73	Leaves not expanded at time of flowering	**Anacardiaceae**
	Leaves present at time of flowering	**74**
74	Leaves entire	**75**
	Leaves lobed or much dissected	**Ranunculaceae**
75	Carpels 5 or fewer	**76**
	Carpels more than 5	**Ranunculaceae**
76	Leaves fleshy	**Crassulaceae**
	Leaves not fleshy	**77**
77	Carpels usually 2–3	**Dilleniaceae**
	Carpels 5	**78**
78	Leaves stipulate; petals white	**Simaroubaceae**
	Leaves exstipulate; petals yellow	**Surianaceae**
79	(1) Petals 2	**Polygalaceae**
	(2) Petals 3	**80**
	(3) Petals 4	**81**
	(4) Petals 5	**147**
	(5) Petals more than 5, or whole perianth petaloid or sepaloid, sometimes in 1 whorl	**347**
80	Leaves simple	**Polygalaceae**
	Leaves compound	**Caesalpiniaceae**
81	(1) Sepals 4, rarely 2–3	**82**
	(2) Sepals 5	**141**
	(3) Sepals 6	**145**
82	Ovary superior	**83**
	Ovary inferior	**126**

83	Leaves radical or alternate	**84**
	Leaves opposite or verticillate	**104**
84	Style 1, with 1 or more stigmas, or stigma sessile	**85**
	Styles more than 1, quite free from one another	**Droseraceae**
85	(1) Stamens 2	**87**
	(2) Stamens 3	**Caesalpiniaceae**
	(3) Stamens 4, alternating with petals	**88**
	(4) Stamens 4, opposite petals	**86**
	(5) Stamens 6	**92**
	(6) Stamens 7 or 8	**93**
	(7) Stamens 10 or more	**100**
86	Placentation basal or free-central	**Myrsinaceae**
	Placentation parietal	**Brassicaceae**
87	Leaves simple, entire or much divided	**Brassicaceae**
	Leaves compound	**Caesalpiniaceae**
88	Climbers with leaf-opposed tendrils	**Vitaceae**
	Plants without tendrils	**89**
89	Leaves simple or absent	**90**
	Leaves compound	**Capparaceae**
90	Herbs	**Brassicaceae**
	Shrubs or trees	**91**
91	Leaves with short, pointed lobes	**Aquifoliaceae**
	Leaves quite entire	**Celastraceae**
92	*(from 85)*	
	Stamens tetradynamous; leaves simple	**Brassicaceae**
	Stamens not tetradynamous; leaves usually compound	**Capparaceae**
93	Stamens free	**94**
	Stamens united	**Meliaceae**
94	Leaves simple or absent	**95**
	Leaves compound	**97**
95	Leaves entire or absent	**96**
	Leaves dissected	**Sapindaceae**
96	Petals glabrous	**Tremandraceae**
	Petals densely hairy inside	**Olacaceae**
97	Leaves 3-foliolate or palmate	**98**
	Leaves pinnate	**99**
98	(1) Ovules 1 in each loculus	**Simaroubaceae**
	(2) Ovules 2 in each loculus	**Burseraceae**
	(3) Ovules indefinite	**Capparaceae**
99	Ovules 1 in each loculus	**Sapindaceae**
	Ovules 2 in each loculus	**Burseraceae**

100	*(from 85)*	
	Flowers in heads or spikes; heads solitary or in racemes	**Mimosaceae**
	Flowers not in heads or spikes	**101**
101	Ovary borne on long stalk (gynophore)	**Capparaceae**
	Ovary sessile	**102**
102	Ovary 1–locular	**Flacourtiaceae**
	Ovary more than 1–locular	**103**
103	Anthers opening by longitudinal slits	**Zygophyllaceae**
	Anthers opening by terminal pores	**Elaeocarpaceae**
104	*(from 83)*	
	Leaves large, palmately lobed	**Aceraceae**
	Leaves otherwise	**105**
105	(1) Stamens 2	**106**
	(2) Stamens 4	**107**
	(3) Stamens 5–8	**112**
	(4) Stamens 10 or indefinite	**123**
106	Flowers in clusters, racemes, or panicles	**Oleaceae**
	Flowers solitary in leaf axils	**Lythraceae**
107	Leaves gland-dotted	**108**
	Leaves not gland-dotted	**109**
108	Style and stigma 1	**Rutaceae**
	Styles or stigmas 4	**Cunoniaceae**
109	Stamens hypogynous	**111**
	Stamens perigynous	**110**
110	Anthers opening by pores; anther-connective with sickle-shaped appendages	**Melastomataceae**
	Anthers opening longitudinally; connective without appendages	**Lythraceae**
111	Style 1	**Celastraceae**
	Styles 4	**Elatinaceae**
112	*(from 105)*	
	Leaves simple or absent	**113**
	Leaves compound	**121**
113	Leaves entire, or with more than 2 lobes	**114**
	Leaves 2–lobed	**Zygophyllaceae**
114	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**115**
115	Ovary half-inferior; margins of petals fringed with long hairs	**Rhizophoraceae**
	Ovary wholly superior; petals not fringed	**116**

116	Style and stigma 1	**117**
	Styles or stigmas more than 1	**120**
117	Flowers hypogynous	**118**
	Flowers perigynous	**119**
118	Leaves in whorls of 3–4	**Tremandraceae**
	Leaves in pairs, opposite	**Rutaceae**
119	Leaves with 2 or more conspicuous longitudinal veins besides midrib	**Melastomataceae**
	Midrib only conspicuous longitudinal vein	**Lythraceae**
120	Leaves with revolute margins; style 1, with 3 branches	**Frankeniaceae**
	Leaf margins not revolute; styles 2 or 4	**Cunoniaceae**
121	*(from 112)*	
	Stamens free	**122**
	Stamens united	**Meliaceae**
122	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**Zygophyllaceae**
123	*(from 105)*	
	Flowers hypogynous, polygamous	**124**
	Flowers perigynous	**125**
124	Stipules absent	**Clusiaceae**
	Stipules present	**Eucryphiaceae**
125	Style and stigma 1	**Lythraceae**
	Styles more than 1	**Cunoniaceae**
126	*(from 82)*	
	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	**127**
127	Stamens indefinite	**128**
	Stamens 10 or fewer	**129**
128	Style and stigma 1	**Lecythidaceae**
	Style with 4 stigmas	**Grossulariaceae**
129	Leaves alternate or radical	**130**
	Leaves opposite or verticillate	**135**
130	Style 1, with 1 or more stigmas	**131**
	Styles several, free	**134**
131	Aquatic herbs with alternate, rosetted floating leaves and opposite submerged leaves	**Trapaceae**
	Trees, shrubs or herbs	**132**
132	(1) Stigma 1	**133**
	(2) Stigmas 2	**Alangiaceae**
	(3) Stigmas 4	**Onagraceae**

133	Ovary 1–locular	**Combretaceae**
	Ovary 4–locular	**Onagraceae**
134	Herbs; flowers very small	**Haloragaceae**
	Shrubs or trees; flowers above 6 mm in diameter	**Grossulariaceae**
135	Style 1, with 1 or more stigmas	**136**
	Styles several, free	**Haloragaceae**
136	Petals fringed with long hairs	**Rhizophoraceae**
	Petals not fringed	**137**
137	Stamens 4	**138**
	Stamens more than 4, usually 8	**139**
138	Aquatic herbs	**Trapaceae**
	Shrubs	**Grossulariaceae**
139	Leaves with 2 or more longitudinal veins besides midrib	**Melastomataceae**
	Midrib the only longitudinal vein	**140**
140	Ovary 1–locular	**Melastomataceae**
	Ovary 4–locular	**Onagraceae**
141	*(from 81)*	
	Ovary 1–2–locular	**142**
	Ovary 3–5–locular	**144**
142	Ovary adnate to one side of calyx-tube	**Chrysobalanaceae**
	Ovary free	**143**
143	(1) Fruit a legume	**Caesalpiniaceae**
	(2) Fruit globose, indehiscent	**Xanthophyllaceae**
	(3) Fruit a capsule	**Zygophyllaceae**
144	(1) Ovary usually 3–locular	**Sapindaceae**
	(2) Ovary 4–locular	**Elaeocarpaceae**
	(3) Ovary 5–locular	**Meliaceae**
145	*(from 81)*	
	Ovary open at top, with sessile stigmas	**Resedaceae**
	Ovary not open at top	**146**
146	Herbs	**Lythraceae**
	Small shrubs	**Saxifragaceae**
147	*(from 79)*	
	(1) Sepals 2	**148**
	(2) Sepals 3	**152**
	(3) Sepals 4	**155**
	(4) Sepals 5 or more, or calyx cup-like with indistinct lobes, or entire in bud	**156**
148	Flowers actinomorphic	**149**
	Flowers zygomorphic	**Caesalpiniaceae**

149	Twiners	**Basellaceae**
	Non-twiners	**150**
150	Herbs	**151**
	Shrubs or trees	**Lecythidaceae**
151	Stamens 5 or fewer; perianth often scarious	**Amaranthaceae**
	Stamens usually more than 5; perianth not scarious; leaves (and often stems) fleshy	**Portulacaceae**
152	Leaves simple or absent	**153**
	Leaves compound	**Caesalpiniaceae**
153	Leaf venation palmate	**Caesalpiniaceae**
	Leaf venation not palmate	**154**
154	(1) Stamens 5	**Hamamelidaceae**
	(2) Stamens 8	**Polygalaceae**
	(3) Stamens indefinite	**Lecythidaceae**
155	Stamens 8–10, free or united	**Caesalpiniaceae**
	Stamens indefinite, united	**Lecythidaceae**
156	Ovary superior	**157**
	Ovary inferior or semi-inferior	**316**
157	Style 1 with simple stigma, or stigma sessile	**158**
	Styles or stigmas more than 1	**251**
158	Leaves opposite or verticillate	**159**
	Leaves alternate, radical, or absent	**178**
159	Leaves gland-dotted	**160**
	Leaves not gland-dotted	**162**
160	Leaves simple	**161**
	Leaves compound	**Rutaceae**
161	Flowers hypogynous	**Rutaceae**
	Flowers perigynous or epigynous	**Myrtaceae**
162	Leaves simple	**163**
	Leaves compound	**175**
163	Leaves with 2 or more conspicuous longitudinal veins besides midrib	**Melastomataceae**
	Midrib only conspicuous longitudinal vein	**164**
164	Stamens 10 or fewer	**165**
	Stamens indefinite	**173**
165	Flowers actinomorphic	**166**
	Flowers zygomorphic	**171**
166	Flowers perigynous	**Lythraceae**
	Flowers not perigynous	**167**
167	(1) Stamens 3	**Hippocrateaceae**
	(2) Stamens 5	**Celastraceae**
	(3) Stamens usually 10	**168**

168	Ovary quite superior	169
	Ovary half-inferior	**Rhizophoraceae**
169	Petals with narrow, pointed lobes	**Rhizophoraceae**
	Petals entire	170
170	Petals clawed; stamens unequal, usually united at base	**Malpighiaceae**
	Petals sessile, shorter than sepals	**Rhizophoraceae**
171	Stamens 5, united; anthers connate round ovary	**Violaceae**
	Stamens 10	172
172	Ovary 1–locular; ovules 2 or more	**Fabaceae**
	Ovary 2–3–locular; 1 ovule in each loculus	**Malpighiaceae**
173	Flowers hypogynous	174
	Flowers perigynous	**Lythraceae**
174	Ovary 1–locular	**Mimosaceae**
	Ovary 2– or more–locular	**Elaeocarpaceae**
175	*(from 162)*	
	Stamens 5	**Meliaceae**
	Stamens more than 5	176
176	Stamens free	177
	Stamens united	**Fabaceae**
177	Ovary 1–locular	**Fabaceae**
	Ovary 2– or more–locular	**Zygophyllaceae**
178	*(from 158)*	
	(1) Stamen 1	179
	(2) Stamens 2–4	180
	(3) Stamens 5	183
	(4) Stamens 6–9 (rarely 5–10)	209
	(5) Stamens 10	215
	(6) Stamens indefinite	235
179	Leaves deeply notched and palmately veined	**Caesalpiniaceae**
	Leaves quite entire and pinnately veined	**Anacardiaceae**
180	Leaves simple	181
	Leaves pinnate or bipinnate	182
181	Leaf venation well-marked and palmate	**Caesalpiniaceae**
	Leaf venation inconspicuous, or leaves absent	**Olacaceae**
182	Stipules present; calyx oblique, of 5 segments; ovary 4–5–locular; fruit a capsule	**Melianthaceae**
	Stipules absent; calyx not oblique, of 5 free sepals; ovary 1–locular; fruit a legume	**Caesalpiniaceae**
183	Leaves simple or absent	184
	Leaves compound	202

184	Leaves bifid; venation palmate	**Caesalpiniaceae**
	Leaves not bifid	**185**
185	(1) Herbs	**186**
	(2) Shrubs, trees or woody climbers; flowers actinomorphic or nearly so	**188**
	(3) Small shrubs; flowers zygomorphic	**Violaceae**
186	(1) Twiners with milky sap	**Cardiopteridaceae**
	(2) Twiners; sap not milky	**Pittosporaceae**
	(3) Plants more or less erect, not twining	**187**
187	Flowers actinomorphic	**Byblidaceae**
	Flowers zygomorphic	**Violaceae**
188	Climbers	**189**
	Non-climbers, more or less erect	**190**
189	Twiners	**Pittosporaceae**
	Climbers with leaf-opposed tendrils	**Vitaceae**
190	Stamens opposite petals	**191**
	Stamens alternate with petals	**192**
191	Each stamen more or less enclosed by small hood-shaped petal	**Rhamnaceae**
	Stamens not enclosed by petals	**Sterculiaceae**
192	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**193**
193	Base of calyx covered by several imbricate sepaloid bracteoles	**Epacridaceae**
	Bracteoles absent or not covering base of calyx	**194**
194	Sepals free	**195**
	Sepals united	**198**
195	(1) Ovary 1–2–locular	**196**
	(2) Ovary 3–locular	**Celastraceae**
	(3) Ovary 5–locular	**Grossulariaceae**
196	Ovules 1 per loculus	**Corynocarpaceae**
	Ovules 2–several per loculus	**197**
197	Ovary 1–2–locular; ovules few to many per loculus	**Pittosporaceae**
	Ovary 1–locular; ovules 2	**Icacinaceae**
198	Ovules 1 per ovary	**199**
	Ovules 2 or more per ovary	**200**
199	Anthers opposite petals	**Opiliaceae**
	Anthers alternate with petals	**Icacinaceae**
200	Ovary 1–locular	**Icacinaceae**
	Ovary 2– or more–locular	**201**
201	Ovary subtended by nectar-secreting disc	**Celastraceae**
	Ovary not subtended by nectar-secreting disc	**Grossulariaceae**

202	*(from 183)*	
	Climbers with leaf-opposed tendrils	**Vitaceae**
	Non-climbers or, if climbing, tendrils not leaf-opposed or tendrils absent	**203**
203	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**204**
204	Stamens 5, staminodes 5	**205**
	Stamens 5, staminodes absent	**206**
205	(1) Trees; leaves pinnate; ovary with 3 parietal placentas; fruit a long 3–angled capsule	**Moringaceae**
	(2) Woody climbers; leaves imparipinnate; ovary with 2 collateral ovules; fruit 1–seeded	**Connaraceae**
	(3) Herbs; leaves 2–foliolate or pinnate; ovary with axile placentas; fruit usually with 2 or more seeds	**Zygophyllaceae**
206	Stamens free	**207**
	Stamens united	**208**
207	Ovary 1–locular; leaves bipinnate	**Mimosaceae**
	Ovary 3–5 locular; leaves pinnate	**Meliaceae**
208	Leaves pinnate	**Meliaceae**
	Leaves bi- or tripinnate	**Vitaceae**
209	*(from 178)*	
	Stamens free	**210**
	Stamens 9, united	**Fabaceae**
210	Leaves simple	**211**
	Leaves compound	**213**
211	Style arising from base of ovary	**Rosaceae**
	Style terminal	**212**
212	Fruit a legume	**Caesalpiniaceae**
	Fruit globose	**Xanthophyllaceae**
213	Ovary 1–locular, usually with more than 2 ovules	**Caesalpiniaceae**
	Ovary 2– or more–locular, with 1 or 2 ovules per loculus	**214**
214	Disc present; stamens inserted within disc	**Sapindaceae**
	Disc absent	**Akaniaceae**
215	*(from 178)*	
	Flowers zygomorphic	**216**
	Flowers actinomorphic or nearly so	**217**
216	Posterior petal enclosed by the remainder, or absent	**Caesalpiniaceae**
	Posterior petal enclosing the remainder in bud	**Fabaceae**
217	Stamens united	**218**
	Stamens free	**222**

218	Climbers	**Connaraceae**
	Non-climbers	**219**
219	(1) Leaves simple	**220**
	(2) Leaves pinnate	**Meliaceae**
	(3) Leaves bi- or tripinnate; ovary 5–locular	**Meliaceae**
	(4) Leaves bipinnate; ovary 1–locular	**Mimosaceae**
220	Staminal tube long and narrow, surrounding style	**Meliaceae**
	Staminal tube short, open	**221**
221	Ovary free; stipules persistent	**Sterculiaceae**
	Ovary adnate to one side of throat of calyx; stipules caducous	**Chrysobalanaceae**
222	Leaves simple or unifoliolate	**223**
	Leaves compound	**228**
223	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**224**
224	Style inserted near base of ovary, hairy	**Simaroubaceae**
	Style terminal	**225**
225	Ovary and back of petals covered with scales; flowers in heads or clusters at end of branchlets	**Rutaceae**
	Not as above	**226**
226	Flowers perigynous; ovary enclosed in hypanthium; stamens borne on hypanthium, sometimes near base	**Lythraceae**
	Not as above; flowers hypogynous	**227**
227	(1) Ovary usually stipitate; ovules several; sepals united	**Caesalpiniaceae**
	(2) Ovary sessile; ovule 1; sepals usually free	**Anacardiaceae**
	(3) Ovary sessile, 5–locular; ovules 1 per loculus; sepals free	**Ochnaceae**
228	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**229**
229	Herbs	**Zygophyllaceae**
	Shrubs or trees	**230**
230	(1) Leaves bipinnate	**Mimosaceae**
	(2) Leaves pinnate; leaflets 2; venation palmate	**Caesalpiniaceae**
	(3) Leaves pinnate; leaflets more than 2 or, if 2, venation pinnate	**231**
231	Ovary 1–locular	**232**
	Ovary 2– or more–locular	**233**
232	(1) Stamens unequal; anthers dehiscing by pores	**Caesalpiniaceae**
	(2) Stamens equal; ovule 1	**Anacardiaceae**
	(3) Stamens equal; ovules more than 1	**Caesalpiniaceae**

233	Ovary 1– or 3–locular, with 1 ovule (rarely 2) per loculus	**Sapindaceae**
	Ovary 4– or 5–locular, with 2 ovules per loculus	**234**
234	Trees or large shrubs; fruit not angular	**Burseraceae**
	Small shrubs; fruit prominently angular	**Zygophyllaceae**
235	*(from 178)*	
	Leaves gland-dotted	**236**
	Leaves not gland-dotted	**237**
236	Flowers hypogynous	**Rutaceae**
	Flowers perigynous or epigynous	**Myrtaceae**
237	Leaves simple, reduced to phyllodes, or absent	**238**
	Leaves compound	**249**
238	(1) Stamens free or only slightly united at base	**239**
	(2) Stamens united into 5 or 10 groups	**Tiliaceae**
	(3) Stamens united into a single group	**248**
239	Flowers small, in globular heads or obloid or cylindrical spikes; stamens much exserted	**Mimosaceae**
	Flowers not as above; stamens usually not exserted	**240**
240	Flowers hypogynous	**241**
	Flowers perigynous	**246**
241	(1) Shrubs; leaves fleshy, entire	**Zygophyllaceae**
	(2) Shrubs, trees or climbers; leaves not fleshy; leaf margins entire, pinnately toothed or lobed	**242**
	(3) Small trees; leaves palmately divided into 5 or 7 lobes	**Bixaceae**
242	Calyx caducous	**Bixaceae**
	Calyx not caducous	**243**
243	Anthers dehiscing by terminal pores or slits	**Elaeocarpaceae**
	Anthers dehiscing longitudinally	**244**
244	Ovary 2– or more–locular	**Tiliaceae**
	Ovary 1–locular	**245**
245	Petals yellow, large	**Dilleniaceae**
	Petals not yellow, small	**Flacourtiaceae**
246	Ovary adnate to one side of throat of calyx	**Chrysobalanaceae**
	Ovary free or completely adnate to calyx	**247**
247	Stamens inserted with petals at rim of hypanthium; ovules 1 or 2 in the ovary	**Rosaceae**
	Stamens inserted on hypanthium below rim (sometimes almost at base); ovules usually numerous	**Lythraceae**
248	Anthers 1–locular	**Malvaceae**
	Anthers 2–locular	**Bombacaceae**

249	*(from 237)*	
	Leaves pinnate or bipinnate	**250**
	Leaves palmate	**Bixaceae**
250	Petals valvate	**Mimosaceae**
	Petals imbricate	**Caesalpiniaceae**
251	*(from 157)*	
	Leaves simple or absent	**252**
	Leaves compound	**307**
252	Leaves opposite or verticillate	**253**
	Leaves alternate, radical, or absent	**274**
253	Stamens 10 or fewer	**254**
	Stamens indefinite	**272**
254	Styles or stigmas 5	**255**
	Styles or stigmas less than 5	**261**
255	Leaves opposite	**256**
	Leaves verticillate	**257**
256	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**258**
257	Floating aquatic plants without roots	**Droseraceae**
	Plants not aquatic	**Caryophyllaceae**
258	Styles 5, free	**259**
	Style 1, with 5 stigmas	**260**
259	Ovary 1–locular	**Caryophyllaceae**
	Ovary 2–5–locular	**Elatinaceae**
260	Ovary 1–locular	**Caryophyllaceae**
	Ovary 3– or more–locular	**Geraniaceae**
261	Leaves palmately lobed	**Aceraceae**
	Leaves otherwise	**262**
262	Styles free	**263**
	Styles united, stigmas 2 or more	**267**
263	Climbers or twiners	**Malpighiaceae**
	Non-climbers, non-twiners	**264**
264	Leaves gland-dotted	**Clusiaceae**
	Leaves not gland-dotted	**265**
265	Mostly herbs; stems usually swollen at nodes	**Caryophyllaceae**
	Shrubs or trees; nodes not swollen	**266**
266	Petals much more than 2 mm long, distinctly clawed	**Malpighiaceae**
	Petals scarcely 2 mm long, sessile or nearly so	**Cunoniaceae**
267	Herbs, non-climbers, non-twiners	**Caryophyllaceae**
	Shrubs, trees, climbers or twiners	**268**

268	(1) Stamens 3	**Hippocrateaceae**
	(2) Stamens 5 or 6	**269**
	(3) Stamens 10	**Malpighiaceae**
269	Stamens opposite to and enclosed in petals	**Rhamnaceae**
	Stamens opposite sepals	**270**
270	Petals clawed, the claws cohering in an angular tube	**Frankeniaceae**
	Petals sessile or if clawed, the claws free	**271**
271	Petals sessile; stamens 5	**Celastraceae**
	Petals clawed; stamens usually more than 5	**Malpighiaceae**
272	*(from 253)*	
	Leaves in whorls of six	**Cunoniaceae**
	Leaves opposite	**273**
273	Juice resinous; stipules absent	**Clusiaceae**
	Juice not resinous; stipules present	**Cistaceae**
274	*(from 252)*	
	Stamens united, often forming a conspicuous staminal tube	**275**
	Stamens free or arising from margin of a small disc	**283**
275	Styles 2 or more, free	**276**
	Style 1, with 2 or more stigmas	**280**
276	Stamens 5, 10, or indefinite	**277**
	Stamens 8	**Aizoaceae**
277	Climbers	**Linaceae**
	Non-climbers	**278**
278	Leaves usually dentate or lobed, with stellate hairs	**Sterculiaceae**
	Leaves entire, glabrous	**279**
279	Stamens 10	**Erythroxylaceae**
	Stamens 4–5	**Linaceae**
280	Petals attached to base of staminal tube; staminal tube usually long; stamens usually indefinite (rarely 10 or fewer); stigmas usually 5 (occasionally fewer or up to 10); herbs, shrubs, or trees	**Malvaceae**
	Not as above	**281**
281	(1) Style branches (or stigmas) 2 or 3; stamens indefinite	**Theaceae**
	(2) Style branches (or stigmas) 2 or 3; stamens 10 or fewer	**Linaceae**
	(3) Style branches (or stigmas) 5	**282**

282	(1) Stamens 5 usually with alternating staminodes; herbs or shrubs; leaves often with stellate hairs	**Sterculiaceae**
	(2) Stamens 5; staminodes 5; glabrous herbs; leaves entire	**Linaceae**
	(3) Stamens 10, usually 3 or 4 without anthers	**Geraniaceae**
	(4) Stamens 10 or indefinite; staminodes sometimes present; leaves often with stellate hairs	**Sterculiaceae**
283	*(from 274)*	
	(1) Stamens 1–3	**284**
	(2) Stamens 5	**285**
	(3) Stamens 6–10	**299**
	(4) Stamens indefinite; flowers hypogynous	**305**
	(5) Stamens indefinite; flowers perigynous	**Rosaceae**
284	Flowers hypogynous	**Tiliaceae**
	Flowers epigynous	**Donatiaceae**
285	Climbers with axillary tendrils	**286**
	Non-climbers, or climbers without axillary tendrils	**287**
286	Corona present within corolla	**Passifloraceae**
	No corona present	**Plumbaginaceae**
287	Styles 2 or more, free	**288**
	Style 1, with 2 or more stigmas	**292**
288	Stamens opposite petals	**289**
	Stamens alternating with petals	**290**
289	Styles 5	**Plumbaginaceae**
	Styles less than 5	**Rhamnaceae**
290	(1) Leaves with conspicuous glandular hairs	**Droseraceae**
	(2) Leaves small, appressed to stem	**Tamaricaceae**
	(3) Not as in (1) or (2) above	**291**
291	Staminodes present; fruit a capsule	**Linaceae**
	Staminodes absent; fruit a drupe	**Dichapetalaceae**
292	Leaves small, appressed to stem	**Tamaricaceae**
	Leaves not appressed to stem	**293**
293	Stamens opposite petals	**Rhamnaceae**
	Stamens alternating with petals	**294**
294	(1) Herbs; stamens 5; staminodes absent	**295**
	(2) Herbs; stamens 5; staminodes 5	**Geraniaceae**
	(3) Shrubs or trees	**296**
295	Fruit a schizocarp	**Stackhousiaceae**
	Fruit a capsule	**Saxifragaceae**
296	Flowers hypogynous	**297**
	Flowers perigynous or epigynous	**Saxifragaceae**

297	Ovary 1–locular	**Icacinaceae**
	Ovary 2– or more–locular	**298**
298	Hypogynous disc present	**Dichapetalaceae**
	Hypogynous disc absent	**Grossulariaceae**
299	*(from 283)*	
	Leaves peltate	**Tropaeolaceae**
	Leaves not peltate	**300**
300	Stamens 8, 6 of them attached to base of corolla	**Polygalaceae**
	Stamens all hypogynous or perigynous	**301**
301	Stamens 10, all with anthers	**302**
	Stamens 7–10; if 10, some without anthers	**Geraniaceae**
302	Style 1, with 2 or more stigmas	**303**
	Styles several, free	**304**
303	Flowers hypogynous; sepals free	**Geraniaceae**
	Flowers perigynous or epigynous; sepals united	**Saxifragaceae**
304	Herbs	**Saxifragaceae**
	Shrubs or trees	**Anacardiaceae**
305	*(from 283)*	
	Sepals valvate or united	**306**
	Sepals imbricate	**Actinidiaceae**
306	Petals deeply incised	**Elaeocarpaceae**
	Petals entire	**Tiliaceae**
307	*(from 251)*	
	Leaves alternate or radical	**308**
	Leaves opposite	**314**
308	Styles or sessile stigmas, free	**309**
	Style 1, with 2 or more stigmas	**312**
309	Herbs	**310**
	Shrubs or trees	**311**
310	Stamens 5	**Droseraceae**
	Stamens 10	**Oxalidaceae**
311	Styles 2; leaflets 2, occasionally one	**Sapindaceae**
	Styles more than 2, or if 2 the leaflets more than 2	**Anacardiaceae**
312	(1) Stamens 3; staminodes 2–5; style petaloid	**Caesalpiniaceae**
	(2) Stamens 5; staminodes absent	**Anacardiaceae**
	(3) Stamens 5, alternating with 5 usually scale-like staminodes	**Geraniaceae**
	(4) Stamens more than 5	**313**
313	(1) Stamens 6–9; stigmas not plumose	**Sapindaceae**
	(2) Stamens 10; stigmas plumose	**Simaroubaceae**
	(3) Stamens indefinite	**Bombacaceae**

314	Leaves with 3 leaflets	**Cunoniaceae**
	Leaves with more than 3 leaflets	**315**
315	(1) Herbs; style simple with 1–5 sessile stigmas	**Zygophyllaceae**
	(2) Herbs or small shrubs; style with 5 short stigmatic branches	**Geraniaceae**
	(3) Trees	**Cunoniaceae**
316	*(from 156)*	
	Stamens 5	**317**
	Stamens more than 5	**327**
317	Stamens opposite petals	**318**
	Stamens alternating with petals	**320**
318	Parasitic shrubs (mistletoes)	**Loranthaceae**
	Plants not parasitic	**319**
319	(1) Leaves gland-dotted	**Myrtaceae**
	(2) Leaves not gland-dotted; stamens attached to petals at their bases	**Alangiaceae**
	(3) Leaves not gland-dotted; stamens free from petals	**Rhamnaceae**
320	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	**321**
321	Herbs, non-climbing, non-twining	**322**
	Shrubs or trees, sometimes climbing or twining	**323**
322	Flowers in umbels or heads; styles or stigmas 2	**Apiaceae**
	Flowers not in umbels or heads; style and stigma 1	**Onagraceae**
323	Flowers in umbels	**326**
	Flowers not in umbels	**324**
324	Leaves compound	**Araliaceae**
	Leaves simple	**325**
325	Flowers in elongated spikes; indumentum stellate	**Hamamelidaceae**
	Flowers racemose or subsolitary; hairs simple or glandular	**Grossulariaceae**
326	Fruit a schizocarp, separating into two flattened mericarps when mature	**Apiaceae**
	Fruit a berry or drupe	**Araliaceae**
327	*(from 316)*	
	Leaves gland-dotted	**328**
	Leaves not gland-dotted	**330**
328	(1) Stamens indefinite	**Myrtaceae**
	(2) Stamens 10, alternating with staminodes	**Myrtaceae**
	(3) Stamens 10 or fewer; staminodes absent	**329**
329	Ovary 1–locular	**Combretaceae**
	Ovary 2– or more–locular	**Myrtaceae**

330	Leaves alternate, radical, or absent	331
	Leaves opposite	338
331	Leaves simple	333
	Leaves compound	332
332	Stamens 2 or 3 opposite each petal	**Flacourtiaceae**
	Stamens indefinite, not regularly opposite petals	**Rosaceae**
333	Style and stigma 1	335
	Styles or stigmas more than 1	334
334	(1) Stamens 6, attached to petals	**Alangiaceae**
	(2) Stamens 10	**Anacardiaceae**
	(3) Stamens indefinite	**Rosaceae**
335	Stamens 10 or fewer	336
	Stamens indefinite	**Rosaceae**
336	Herbs	**Onagraceae**
	Shrubs (sometimes climbing) or trees	337
337	Ovary 1–locular	**Combretaceae**
	Ovary 2– or more–locular	**Grossulariaceae**
338	Leaves simple or absent	339
	Leaves compound	346
339	Leaves with several conspicuous longitudinal veins	**Melastomataceae**
	Midrib the only conspicuous longitudinal vein	340
340	Stamens usually 10, rarely up to 13	341
	Stamens indefinite	**Punicaceae**
341	Style 1, stigmas 1 or 2	342
	Styles 3	345
342	Leaves unequal, one of each pair much larger than other; anthers with conspicuous appendages	**Melastomataceae**
	Leaves of each pair equal; anthers without appendages	343
343	Ovary 1–locular	**Combretaceae**
	Ovary 2– or more–locular	344
344	Trees of sea-shores or salt creeks	**Rhizophoraceae**
	Plants not growing in salt water	**Saxifragaceae**
345	Petals sessile or with very short claws	**Saxifragaceae**
	Petals with slender claws	**Malpighiaceae**
346	Leaves petiolate	**Cunoniaceae**
	Leaves sessile	**Saxifragaceae**
347	*(from 79)*	
	Flowers with one or more long spurs	**Ranunculaceae**
	Flowers without a spur	348

348	(1) Sepals 2; style short or absent; stigmas usually confluent	**Papaveraceae**
	(2) Sepals 2; styles several, free, or style 1 with several free stigmas; plants more or less fleshy	**Portulacaceae**
	(3) Sepals more than 2, or whole perianth petaloid or sepaloid	**349**
349	Ovary superior	**350**
	Ovary inferior	**370**
350	Aquatic herbs with floating or submerged leaves	**Nymphaeaceae**
	Herbs (not aquatic), shrubs, or trees	**351**
351	Leaves alternate	**352**
	Leaves opposite or verticillate	**366**
352	Climbers	**353**
	Non-climbers	**355**
353	Tendril climbers	**Passifloraceae**
	Not tendril climbers	**354**
354	Branches spiny	**Cactaceae**
	Branches not spiny	**Menispermaceae**
355	One perfect stamen (much longer than the others) and usually 4 or more imperfect stamens	**Anacardiaceae**
	Perfect stamens 5 or more	**356**
356	Leaves simple or absent	**357**
	Leaves compound	**365**
357	Flowers hypogynous	**359**
	Flowers perigynous	**358**
358	Stamens hypogynous or inserted low in hypanthium	**Lythraceae**
	Stamens inserted on rim of hypanthium	**Rosaceae**
359	Herbs	**360**
	Shrubs or trees	**361**
360	Ovary open at top, with sessile stigmas	**Resedaceae**
	Ovary closed; style present	**Amaranthaceae**
361	Stamens 6–9	**362**
	Stamens 10 or indefinite	**363**
362	Plants spiny	**Berberidaceae**
	Plants without spines	**Flacourtiaceae**
363	Perianth segments 3 + 3 + 3; styles indefinite	**Magnoliaceae**
	Sepals 5 or more; styles or stigmas 5 or fewer	**364**
364	Bracteoles present, merging into sepals	**Theaceae**
	Bracteoles absent or small	**Flacourtiaceae**
365	Stamens 6	**Berberidaceae**
	Stamens 10	**Mimosaceae**

366	*(from 351)*	
	Leaves simple	**367**
	Leaves compound, with 3 leaflets (each pair looking like a whorl of 6 leaves)	**Cunoniaceae**
367	Ovary 3–6–locular	**368**
	Ovary 10–15–locular	**Sonneratiaceae**
368	Leaves with 5–7 conspicuous longitudinal veins	**Melastomataceae**
	Midrib the only conspicuous longitudinal vein	**369**
369	Stamens inserted on the hypanthium; anthers opening longitudinally	**Lythraceae**
	Stamens at base of hypanthium; anthers opening by terminal pores	**Melastomataceae**
370	*(from 349)*	
	Aquatic herbs	**Nymphaeaceae**
	Herbs (not aquatic), shrubs, or trees	**371**
371	(1) Leaves alternate or clustered	**372**
	(2) Leaves opposite	**380**
	(3) Leaves absent	**Cactaceae**
372	Branches spiny	**373**
	Branches without spines	**374**
373	Plants fleshy, leafless	**Cactaceae**
	Plants woody, with leaves	**Punicaceae**
374	Plants parasitic (mistletoes)	**Loranthaceae**
	Plants not parasitic	**375**
375	Leaves fleshy	**Aizoaceae**
	Leaves not fleshy	**376**
376	Leaves simple	**377**
	Leaves palmate	**Araliaceae**
377	Stamens (+ staminodes if present) indefinite	**378**
	Stamens less than 10	**379**
378	Style 1, stigma 1	**Punicaceae**
	Stigmas indefinite, sessile on flat surface of ovary	**Eupomatiaceae**
379	(1) Style 1, stigmas 2	**Alangiaceae**
	(2) Styles or stigmas 3–5	**Flacourtiaceae**
	(3) Stigma 1, sessile	**Combretaceae**
380	*(from 371)*	
	Leaves fleshy; stigmas 5	**Aizoaceae**
	Leaves not fleshy; stigmas 1 or 2	**381**
381	(1) Petals absent; leaves gland-dotted	**Myrtaceae**
	(2) Petals absent; leaves not gland-dotted	**Sonneratiaceae**
	(3) Petals present	**382**

382	Leaves with 5–7 conspicuous longitudinal veins	**Melastomataceae**
	Midrib the only conspicuous longitudinal vein	**383**
383	Sepals and petals each indefinite	**Rhizophoraceae**
	Sepals and petals each less than 10	**384**
384	Stamens less than 20	**385**
	Stamens 20 or more	**Punicaceae**
385	Ovary 1–locular, with about 10 ovules	**Combretaceae**
	Ovary 2–5–locular, with 1–2 ovules per loculus	**Rhizophoraceae**
386	*(from 11)*	
	Flowers unisexual	**387**
	Flowers mostly bisexual	**400**
387	Leaves opposite	**388**
	Leaves alternate	**391**
388	Ovary superior	**389**
	Ovary inferior	**Rubiaceae**
389	Gynoecium apocarpous	**Monimiaceae**
	Gynoecium syncarpous or carpel 1	**390**
390	Fruit a berry	**Theaceae**
	Fruit 1–4 nutlets	**Lamiaceae**
391	Perianth segments in 2 whorls	**394**
	Perianth segments in 1 whorl	**392**
392	Ovary inferior	**Araliaceae**
	Ovary superior	**393**
393	Stamens 6 or more in regular series around a disc-like axis; perianth shallow, cup-shaped, entire to slightly lobed	**Gyrostemonaceae**
	Stamens 1–many, not arranged as above; sepals evidently lobed	**Euphorbiaceae**
394	Sepals 4; petals 4	**395**
	Sepals and petals each 5 or more	**396**
395	Climbers	**Menispermaceae**
	Non-climbers	**Ebenaceae**
396	Ovary superior	**397**
	Ovary inferior	**399**
397	Stamens 5 in male flowers	**398**
	Stamens usually 10 in male flowers	**Ebenaceae**
398	Fruit a capsule	**Solanaceae**
	Fruit a nut or drupe	**Olacaceae**
399	Placentation parietal	**Cucurbitaceae**
	Placentation axile	**Campanulaceae**

400	*(from 386)*	
	Ovary superior	**401**
	Ovary inferior or half-inferior	**544**
401	(1) Stamens 2	**402**
	(2) Stamens 3	**Olacaceae**
	(3) Stamens 4	**418**
	(4) Stamens 5	**463**
	(5) Stamens more than 5	**529**
402	Ovary entire or slightly lobed	**403**
	Ovary divided into (usually 4) free or nearly free segments	**Lamiaceae**
403	Flowers actinomorphic	**404**
	Flowers zygomorphic	**409**
404	Leaves simple or absent	**405**
	Leaves compound	**Oleaceae**
405	(1) Corolla-lobes 4	**Oleaceae**
	(2) Corolla-lobes 5	**406**
	(3) Corolla-lobes more than 5	**Oleaceae**
406	(1) Herbs	**Scrophulariaceae**
	(2) Shrubs or undershrubs	**407**
	(3) Climbers	**Oleaceae**
407	Flowers in long terminal spikes	**Verbenaceae**
	Flowers not in spikes	**408**
408	Style minutely notched at top	**Oleaceae**
	Style deeply divided into 2 branches	**Verbenaceae**
409	Bracteoles large, more or less covering calyx	**Acanthaceae**
	Bracteoles absent or small	**410**
410	Calyx divided into 2 lobes or segments	**411**
	Calyx divided into more than 2 lobes or segments	**412**
411	Leaves opposite	**Verbenaceae**
	Leaves, if present, alternate or radical	**Lentibulariaceae**
412	Leaves radical or alternate	**413**
	Leaves opposite	**414**
413	Ovary 1–locular; placentation parietal	**Gesneriaceae**
	Ovary 2–locular; placentation axile	**Solanaceae**
414	Leaves with viscid hairs	**Pedaliaceae**
	Leaves glabrous or hairs, if present, not viscid	**415**
415	Ovary 1–locular	**Gesneriaceae**
	Ovary 2– or more–locular	**416**
416	Seeds endospermic	**Scrophulariaceae**
	Seeds not endospermic	**417**

417	Fruit a capsule	**Acanthaceae**
	Fruit a drupe or divided into nutlets	**Verbenaceae**
418	*(from 401)*	
	Ovary apocarpous	**Monimiaceae**
	Ovary syncarpous or carpel 1	**419**
419	Flowers actinomorphic or nearly so	**420**
	Flowers zygomorphic	**445**
420	(1) Leaves alternate, bipinnate	**Mimosaceae**
	(2) Leaves alternate or absent in mature plant, not bipinnate	**422**
	(3) Leaves opposite or verticillate	**432**
	(4) Leaves radical	**421**
421	Sepals 4, free; petals 4, united	**Plantaginaceae**
	Sepals 5, free; petals 5, united	**Acanthaceae**
422	(1) Corolla-lobes 3	**Polygalaceae**
	(2) Corolla-lobes 4	**423**
	(3) Corolla-lobes 5	**427**
423	Stamens alternating with corolla-lobes	**424**
	Stamens opposite corolla-lobes	**426**
424	Twining plants	**425**
	Prostrate annuals	**Boraginaceae**
425	Leaves absent	**Cuscutaceae**
	Leaves present	**Cardiopteridaceae**
426	Ovary 1–locular with several ovules	**Myrsinaceae**
	Ovary 2–locular with 1 ovule per loculus	**Sapotaceae**
427	Leaves absent	**Cuscutaceae**
	Leaves present	**428**
428	Leaves with viscid hairs	**429**
	Leaves glabrous or hairs, if present, not viscid	**430**
429	Seeds endospermic	**Solanaceae**
	Seeds non-endospermic	**Pedaliaceae**
430	Anthers connivent around the style	**Solanaceae**
	Anthers not connivent	**431**
431	Fruit a drupe	**Myoporaceae**
	Fruit a capsule or berry	**Solanaceae**
432	*(from 420)*	
	Ovary divided into (usually 4) separate segments	**433**
	Ovary entire or lobed	**434**
433	Style terminal	**Verbenaceae**
	Style gynobasic, rarely terminal	**Lamiaceae**
434	Sepals 4	**435**
	Sepals 5 or more, or calyx 2–lipped or truncate	**440**

435	(1) Ovary 1–locular, with 2 parietal placentas	**Gentianaceae**
	(2) Ovary 2–locular	**436**
	(3) Ovary 4–locular	**Verbenaceae**
436	Herbs	**437**
	Shrubs or trees	**Loganiaceae**
437	Leaves in whorls, usually of 3	**Scrophulariaceae**
	Leaves opposite	**438**
438	Ovary quite superior	**439**
	Ovary half-inferior	**Rubiaceae**
439	Capsule circumscissile	**Plantaginaceae**
	Capsule septicidal	**Loganiaceae**
440	Corolla 4–lobed	**Verbenaceae**
	Corolla 5–lobed	**441**
441	Leaves simple or absent	**442**
	Leaves compound	**Bignoniaceae**
442	Bracteoles large, more or less enclosing calyx	**Acanthaceae**
	Bracteoles absent or not enclosing calyx	**443**
443	Placentas axile	**444**
	Placentas parietal	**Gesneriaceae**
444	(1) Ovary 2–locular, with several ovules; herbs or small shrubs	**Scrophulariaceae**
	(2) Ovary 2–locular, with numerous ovules; trees	**Bignoniaceae**
	(3) Ovary 4–locular, with 1 ovule per loculus	**Verbenaceae**
445	*(from 419)*	
	(1) Leaves all simple or reduced to scales	**448**
	(2) Leaves all compound	**460**
	(3) Leaves variable	**446**
446	Leaves opposite, the upper ones sometimes becoming alternate	**447**
	Leaves mostly in whorls of 3	**Bignoniaceae**
447	Upper leaves simple, lower leaves compound; ovary 2– or 4–locular with 1–many ovules per loculus	**Pedaliaceae**
	Leaves very variable, simple or with 3–5 leaflets; ovary 2–locular with 2 ovules per loculus	**Verbenaceae**
448	Leaves reduced to scales; plants without chlorophyll	**Orobanchaceae**
	Leaves not reduced to scales; plants green	**449**
449	(1) Leaves radical	**Scrophulariaceae**
	(2) Upper leaves alternate, lower leaves opposite	**450**
	(3) Leaves all alternate	**451**
	(4) Leaves all opposite or verticillate	**456**
450	Ovary 2–locular	**Scrophulariaceae**
	Ovary 4–locular	**Pedaliaceae**

451	Calyx of 3 outer and 2 inner sepals, all free; petals 3, united	**Polygalaceae**
	Calyx of 5 free or united sepals in 1 whorl; petals 5, united	**452**
452	Ovary 2–locular	**453**
	Ovary 4–locular	**Myoporaceae**
453	Herbs (sometimes climbing)	**454**
	Shrubs or small trees	**455**
454	Corolla actinomorphic or nearly so, usually spreading	**Solanaceae**
	Corolla 2–lipped	**Scrophulariaceae**
455	Stigmas 2; fruit a capsule or berry	**Solanaceae**
	Stigma 1; fruit a drupe	**Myoporaceae**
456	Ovary divided into 4 nearly separate segments at maturity	**Lamiaceae**
	Ovary simple or lobed	**457**
457	(1) Ovary 1–locular; ovules numerous	**Gesneriaceae**
	(2) Ovary 2–locular	**458**
	(3) Ovary 4–locular with 1 ovule per loculus	**Verbenaceae**
	(4) Ovary 8–locular with 1 ovule per loculus	**Pedaliaceae**
458	Bracteoles conspicuous, often more or less covering calyx	**Acanthaceae**
	Bracteoles small or absent	**459**
459	(1) Undershrubs, shrubs or woody vines, rarely trees; ovules 1 or 2 per loculus	**Verbenaceae**
	(2) Herbs or small shrubs; ovules 2 or more per loculus	**Scrophulariaceae**
	(3) Small or large trees; ovules numerous	**Bignoniaceae**
460	*(from 445)*	
	Climbers, usually woody	**Bignoniaceae**
	Shrubs or trees	**461**
461	(1) Leaves with 3 leaflets; fifth stamen represented by a staminode	**Bignoniaceae**
	(2) Leaves with 3 leaflets; fifth stamen absent	**Verbenaceae**
	(3) Leaves with more than 3 leaflets	**462**
462	Ovules 2 per loculus; fifth stamen absent	**Verbenaceae**
	Ovules more than 2 per loculus; fifth stamen usually represented by a staminode	**Bignoniaceae**
463	*(from 401)*	
	Latex present	**464**
	Latex absent	**471**
464	(1) Leaves alternate	**465**
	(2) Leaves opposite or verticillate	**470**
	(3) Leaves absent	**Asclepiadaceae**

465	Twiners	**466**
	Non-twiners	**467**
466	Fruits winged	**Cardiopteridaceae**
	Fruits not winged	**Convolvulaceae**
467	Flowers actinomorphic	**468**
	Flowers zygomorphic	**Campanulaceae**
468	Anthers connivent around or above stigma	**Apocynaceae**
	Anthers free	**469**
469	Stamens alternating with lobes or angles of corolla	**Convolvulaceae**
	Stamens opposite corolla-lobes	**Sapotaceae**
470	Stamens lacking a coronal appendage; pollen grains single	**Apocynaceae**
	Stamens mostly with a coronal appendage; pollen grains cohering in tetrads or pollinia	**Asclepiadaceae**
471	Leafless parasites	**Cuscutaceae**
	Leafy plants	**472**
472	Gynoecium apocarpous or divided into 2 or more free segments	**473**
	Gynoecium syncarpous, the ovary entire or lobed, or carpel 1	**477**
473	(1) Leaves alternate or radical	**474**
	(2) Leaves opposite or verticillate	**476**
	(3) Leaves absent	**Asclepiadaceae**
474	Inflorescence a monochasial cyme, uncoiling as the flowers open	**Boraginaceae**
	Inflorescence not as above	**475**
475	Plants slender, creeping perennials, rooting at nodes	**Convolvulaceae**
	Plants more or less erect	**Boraginaceae**
476	Perianth segments (calyx plus corolla) 10 or fewer	**Apocynaceae**
	Perianth segments about 15	**Monimiaceae**
477	(1) Leaves verticillate	**480**
	(2) Leaves opposite	**481**
	(3) Leaves alternate, in alternate pairs, or clustered	**478**
478	Leaves compound	**479**
	Leaves simple	**496**
479	Leaves stipulate	**Mimosaceae**
	Leaves exstipulate	**Leeaceae**
480	Shrubs or trees	**Apocynaceae**
	Floating herbs	**Droseraceae**
481	Flowers actinomorphic	**482**
	Flowers zygomorphic	**494**

482	Leaves simple	**483**
	Leaves compound	**Bignoniaceae**
483	(1) Style 1, with 1 or 2 stigmas	**484**
	(2) Style 1, with 3 branches	**493**
	(3) Style 1, with 4 branches	**Polemoniaceae**
	(4) Styles or style branches 5	**Plumbaginaceae**
	(5) Style 1, apex divided into many minute stigmatic branches	**Nyctaginaceae**
484	Inflorescence a monochasial cyme	**Boraginaceae**
	Inflorescence not a monochasial cyme	**485**
485	Anthers cohering about style	**486**
	Anthers quite free	**488**
486	Herbs	**Caryophyllaceae**
	Shrubs	**487**
487	Leaves opposite	**Apocynaceae**
	Leaves alternate	**Solanaceae**
488	Stamens alternating with corolla-lobes	**489**
	Stamens opposite corolla-lobes	**Primulaceae**
489	Ovary 1–locular	**490**
	Ovary 2– or 4–locular	**491**
490	Stipules small, scarious	**Caryophyllaceae**
	Stipules absent	**Gentianaceae**
491	Plants (including the inflorescence) densely covered with cottony or woolly hairs	**Verbenaceae**
	Not as above	**492**
492	Leaves all opposite, usually stipulate	**Loganiaceae**
	Leaves on non-flowering parts alternate, exstipulate	**Solanaceae**
493	Stamens free from corolla	**Frankeniaceae**
	Stamens epipetalous	**Polemoniaceae**
494	*(from 481)*	
	Leaves simple	**495**
	Leaves compound	**Bignoniaceae**
495	Ovary 4– or occasionally 2–locular	**Verbenaceae**
	Ovary 1–locular; leaves with viscid hairs	**Pedaliaceae**
496	*(from 478)*	
	Petals 3	**Polygalaceae**
	Petals 4 or 5	**497**
497	Style with indusium	**498**
	No indusium present	**499**
498	Corolla actinomorphic or nearly so	**Brunoniaceae**
	Corolla zygomorphic, usually split down one side	**Goodeniaceae**

499	Flowers zygomorphic	**Solanaceae**
	Flowers actinomorphic	**500**
500	(1) Stamens free from petals	**501**
	(2) Stamens free from but usually detached with petals	**Pittosporaceae**
	(3) Stamens distinctly epipetalous, though sometimes attached near the base of corolla-tube	**509**
501	Stigmas 1 or 2	**502**
	Stigmas 4 or 5	**Plumbaginaceae**
502	Stamens opposite corolla-lobes	**503**
	Stamens alternating with corolla-lobes	**505**
503	Nectar-secreting disc conspicuous, embedding base of ovary	**Olacaceae**
	Nectar-secreting disc absent	**504**
504	Ovary 1–locular with several ovules	**Myrsinaceae**
	Ovary 2– or more–locular with 1 ovule per loculus	**Sapotaceae**
505	Herbs	**506**
	Trees, shrubs, climbers, or twiners	**507**
506	Leaves with glandular hairs; corolla segments only united in short ring at base	**Byblidaceae**
	Leaves not as above; corolla segments cohering to form a tube, but free right at the base	**Stackhousiaceae**
507	Calyx covered at base with usually numerous imbricate sepaloid bracteoles	**Epacridaceae**
	Bracteoles absent, or not covering base of calyx	**508**
508	Anthers versatile; ovules 1 or 2 in ovary	**Olacaceae**
	Anthers not versatile; ovules more than two in ovary	**Pittosporaceae**
509	*(from 500)*	
	Inflorescence a monochasial cyme	**510**
	Inflorescence not a monochasial cyme	**512**
510	Style 1, with 1 or more stigmas	**511**
	Styles 2, free	**Hydrophyllaceae**
511	Fruit a capsule or berry	**Solanaceae**
	Fruit a drupe or divided into nutlets	**Boraginaceae**
512	(1) Style 1, with 1 or 2 stigmas, or stigma sessile	**513**
	(2) Style 1, with 3 stigmas	**Polemoniaceae**
	(3) Style 1, with 4 stigmas	**527**
	(4) Style 1, with 5 stigmas	**Plumbaginaceae**
	(5) Style 1, with 6–8 stigmas	**Convolvulaceae**
	(6) Styles 2, free	**528**
	(7) Styles 5, free	**Plumbaginaceae**
513	Stamens opposite corolla-lobes	**514**
	Stamens alternating with corolla-lobes	**516**

514	Herbs	**Primulaceae**
	Shrubs or trees	**515**
515	Ovary 1–locular, with central placenta	**Myrsinaceae**
	Ovary 2– or more–locular	**Sapotaceae**
516	Leaves simple or absent from mature plant	**517**
	Leaves compound	**525**
517	Herbs, growing in marshes or in water	**Menyanthaceae**
	Herbs (not aquatic), shrubs or trees, sometimes climbers	**518**
518	Base of calyx more or less covered by imbricate bracts and bracteoles; bracteoles sometimes only 2	**Epacridaceae**
	Bracteoles absent, or not covering base of calyx	**519**
519	Climbers, twiners, or prostrate plants	**520**
	Plants more or less erect	**521**
520	Anthers connivent in cone around style, dehiscing by pores or slits; ovary 2–locular, usually with many ovules	**Solanaceae**
	Anthers not connivent; ovary 1–2–locular; ovules 2 or 4 per loculus	**Convolvulaceae**
521	(1) Herbs (sometimes coarse), usually annual; ovules 2 or more per loculus	**Solanaceae**
	(2) Coarse annuals; ovules 1 per loculus	**Boraginaceae**
	(3)Shrubs or small trees	**522**
522	(1) Ovary 1–locular	**Monimiaceae**
	(2) Ovary 2–locular	**523**
	(3) Ovary 3–locular	**Solanaceae**
	(4) Ovary 4–locular	**524**
	(5) Ovary usually 5–locular	**Epacridaceae**
523	(1) Ovules 1 per loculus	**Myoporaceae**
	(2) Ovules 2 per loculus	**Boraginaceae**
	(3) Ovules more than 2 per loculus	**Solanaceae**
524	Fruit a drupe or nut; ovules 1 per loculus	**Boraginaceae**
	Fruit a berry or capsule; ovules usually more than 1 per loculus	**Solanaceae**
525	Tendril climbers	**Polemoniaceae**
	Not tendril climbers but sometimes twiners	**526**
526	Leaves palmate	**Convolvulaceae**
	Leaves pinnate	**Solanaceae**
527	*(from 512)*	
	Usually annuals, with slender creeping or trailing stems; ovary 2–locular	**Convolvulaceae**
	Tall shrubs or trees; ovary 4–locular	**Boraginaceae**

528	*(from 512)*	
	(1) Each of the 2 styles divided into 2 branches	**Convolvulaceae**
	(2) Each style simple; ovary 2–locular, with numerous ovules	**Hydrophyllaceae**
	(3) Each style simple; ovary 2–locular, with 2 ovules per loculus	**Convolvulaceae**
529	*(from 401)*	
	Latex present	**Sapotaceae**
	Latex absent	**530**
530	(1) Leaves simple or reduced to phyllodes	**531**
	(2) Leaves pinnatisect	**Ranunculaceae**
	(3) Leaves compound	**541**
531	Gynoecium apocarpous	**532**
	Gynoecium syncarpous or carpel 1	**533**
532	Style 1	**Rutaceae**
	Styles as many as carpels	**Crassulaceae**
533	Perfect stamens alternating with staminodes (sometimes scale-like)	**Sapotaceae**
	Stamens all perfect	**534**
534	Stamens 10 or fewer	**535**
	Stamens indefinite	**539**
535	Style 1, the apex divided into many minute stigmatic branches	**Nyctaginaceae**
	Styles or stigmas 5 or fewer, apex not as above	**536**
536	Stamens free	**537**
	Stamens united	**Polygalaceae**
537	Stamens free from corolla, hypogynous	**Ericaceae**
	Stamens epipetalous	**538**
538	Style and stigma 1	**Solanaceae**
	Styles or stigmas 2 or more	**Ebenaceae**
539	Ovary of 1 carpel, 1–locular; style and stigma 1	**Mimosaceae**
	Ovary syncarpous, mostly 3–5–locular; styles or stigmas 2 or more	**540**
540	Pedicel with a pair of bracts	**Theaceae**
	Pedicel lacking bracts	**Actinidiaceae**
541	*(from 530)*	
	Leaves bipinnate	**Mimosaceae**
	Leaves pinnate or 3–foliolate	**542**
542	Gynoecium apocarpous	**Crassulaceae**
	Gynoecium syncarpous or carpel 1	**543**
543	Style 1; ovary 1–locular	**Mimosaceae**
	Styles 3–5; ovary 3–5–locular	**Oxalidaceae**

544	*(from 400)*	
	Leaves opposite or verticillate	**545**
	Leaves alternate, radical, or absent	**559**
545	(1) Petals 4	**546**
	(2) Petals 5	**549**
	(3) Petals more than 5	**557**
546	Leaves simple	**547**
	Leaves compound	**Caprifoliaceae**
547	Stamens free from petals	**548**
	Stamens epipetalous	**Rubiaceae**
548	Ovary 1–locular	**Grossulariaceae**
	Ovary 2–5–locular	**Campanulaceae**
549	(1) Stamen 1	**Valerianaceae**
	(2) Stamens 4	**550**
	(3) Stamens 5	**552**
550	Flowers in heads surrounded by involucre of bracts	**Dipsacaceae**
	Flowers not in heads	**551**
551	Herbs	**Gesneriaceae**
	Shrubs	**Caprifoliaceae**
552	Plants parasitic (mistletoes)	**Loranthaceae**
	Plants not parasitic	**553**
553	Stamens epipetalous	**555**
	Stamens free from petals	**554**
554	Style expanded into an indusium	**Goodeniaceae**
	Style without indusium	**Campanulaceae**
555	Flowers actinomorphic	**556**
	Flowers zygomorphic	**Caprifoliaceae**
556	Leaves stipulate	**Rubiaceae**
	Leaves exstipulate	**Caprifoliaceae**
557	*(from 545)*	
	Style 1, stigmas 1 or 2	**558**
	Styles or stigmas 3 or 5	**Rubiaceae**
558	Plants parasitic (mistletoes)	**Loranthaceae**
	Plants not parasitic	**Rubiaceae**
559	*(from 544)*	
	Plants parasitic (mistletoes)	**Loranthaceae**
	Plants not parasitic	**560**
560	(1) Stamens 2; gynandrous	**Stylidiaceae**
	(2) Stamens 3	**Cucurbitaceae**
	(3) Stamens 4	**Campanulaceae**
	(4) Stamens 5	**561**
	(5) Stamens more than 5	**569**

561	Style expanded into an indusium	**Goodeniaceae**
	Style without indusium	**562**
562	Flowers actinomorphic	**563**
	Flowers zygomorphic, corolla-tube usually split down one side	**Campanulaceae**
563	Prostrate plants or climbers; tendrils large	**Cucurbitaceae**
	Non-climbers; tendrils absent	**564**
564	Stamens alternating with corolla-lobes	**565**
	Stamens opposite corolla-lobes	**568**
565	Ovary 1–locular	**Menyanthaceae**
	Ovary 2– or more–locular	**566**
566	Stems more or less succulent, hollow; flowers in dense spikes	**Sphenocleaceae**
	Stems not succulent, solid; flowers racemose or axillary	**567**
567	Fruit a capsule	**Campanulaceae**
	Fruit a berry	**Epacridaceae**
568	(1) Herbs	**Primulaceae**
	(2) Trees or climbers; stigma 1	**Myrsinaceae**
	(3) Trees; stigmas 3	**Alangiaceae**
569	(1) Stamens 6	**Alangiaceae**
	(2) Stamens 10	**Ericaceae**
	(3) Stamens indefinite	**570**
570	Leaves persistent	**571**
	Leaves, if present, caducous	**Cactaceae**
571	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	**Symplocaceae**
572	*(from 10)*	
	Flowers unisexual	**573**
	Flowers mostly bisexual	**647**
573	Leafless stem parasite embedded in host; only the flowers emergent	**Rafflesiaceae**
	Not an embedded parasite (though sometimes leafless)	**574**
574	Leaves or scales in whorls of 3 or more	**575**
	Leaves or scales alternate, opposite, or absent	**577**
575	Aquatic herbs	**576**
	Shrubs or trees	**Casuarinaceae**
576	Ovary inferior	**Haloragaceae**
	Ovary superior	**Ceratophyllaceae**
577	Latex present	**578**
	Latex absent	**580**

578	Separate male and female flowers inside pear-shaped receptacle which opens by narrow aperture at top	**Moraceae**
	Not as above	**579**
579	Leaves stipulate; ovary 1–locular with 1 ovule	**Moraceae**
	Leaves exstipulate; ovary 2– or more–locular	**Euphorbiaceae**
580	(1) Perianth segments 2	**581**
	(2) Perianth segments 3	**586**
	(3) Perianth segments 4	**595**
	(4) Perianth segments 5 or more, or perianth obscurely lobed or truncate	**614**
581	Ovary superior	**582**
	Ovary inferior	**585**
582	Climbers	**Menispermaceae**
	Non-climbers	**583**
583	Ovary 1–locular; styles 2	**584**
	Ovary 2–3–locular; styles 2 or 3	**Euphorbiaceae**
584	Leaves stipulate	**Urticaceae**
	Leaves exstipulate	**Chenopodiaceae**
585	Flowers minute, in heads, surrounded by involucre of bracts	**Asteraceae**
	Flowers not in heads	**Gunneraceae**
586	Ovary inferior	**587**
	Ovary superior	**588**
587	Herbs	**Gunneraceae**
	Parasitic shrubs (mistletoes)	**Viscaceae**
588	Succulent root parasites without chlorophyll, 5–10 cm high with scale-like leaves	**Balanophoraceae**
	Herbs, shrubs, or trees, not parasitic	**589**
589	Style or stigma 1	**590**
	Styles or style branches 2 or more	**593**
590	Stigma penicillate	**Urticaceae**
	Stigma not penicillate	**591**
591	Leaves simple	**592**
	Leaves compound	**Sapindaceae**
592	Leaves with 7–20 primary veins on each side of midrib	**Myristicaceae**
	Midrib the only prominent vein, if any	**Santalaceae**
593	Ovary 1–locular, with 1 ovule	**594**
	Ovary 2–3–locular	**Euphorbiaceae**
594	Leaves stipulate	**Polygonaceae**
	Leaves exstipulate	**Amaranthaceae**

595	*(from 580)*	
	(1) Leafless succulents, parasitic on roots	**Balanophoraceae**
	(2) Shrubs parasitic on stems (mistletoes)	**Viscaceae**
	(3) Plants not parasitic	**596**
596	Ovary or gynoecium superior	**597**
	Ovary inferior	**612**
597	Gynoecium apocarpous	**598**
	Gynoecium syncarpous or carpel 1	**601**
598	Styles free	**599**
	Styles 4, connate	**Sterculiaceae**
599	Leaves opposite	**600**
	Leaves alternate	**Phytolaccaceae**
600	Leaves simple	**Monimiaceae**
	Leaves compound	**Ranunculaceae**
601	Leaf terminating in a tendril or pitcher provided with a lid	**Nepenthaceae**
	Leaf not terminating in a tendril or pitcher, or leaves absent	**602**
602	Styles or stigmas penicillate	**Urticaceae**
	Neither styles nor stigmas penicillate	**603**
603	(1) Style 1	**605**
	(2) Styles 2	**Ulmaceae**
	(3) Styles 3–6	**604**
604	Placentation axile	**Euphorbiaceae**
	Placentation parietal	**Flacourtiaceae**
605	Leaves simple or absent	**606**
	Leaves compound	**611**
606	(1) Leaves alternate, without stinging hairs, or leaves absent	**607**
	(2) Leaves alternate, with stinging hairs	**Urticaceae**
	(3) Leaves opposite	**Urticaceae**
607	(1) Stamens 2 in male flowers	**Thymelaeaceae**
	(2) Stamens usually 4 in male flowers	**608**
	(3) Stamens 6 in male flowers	**Lauraceae**
	(4) Stamens 10 or indefinite in male flowers	**610**
608	Leaves not expanded at time of flowering; stigma sessile	**Santalaceae**
	Leaves present at time of flowering	**609**
609	Leaves stipulate	**Urticaceae**
	Leaves exstipulate	**Phytolaccaceae**
610	Ovary glabrous	**Flacourtiaceae**
	Ovary with hooked bristles	**Phytolaccaceae**

611	Leaves stipulate	**Rosaceae**
	Leaves exstipulate	**Sapindaceae**
612	*(from 596)*	
	Herbs	**Haloragaceae**
	Shrubs or trees	**613**
613	Fruit a nut	**Fagaceae**
	Fruit a capsule	**Datiscaceae**
614	*(from 580)*	
	Ovary or gynoecium superior	**615**
	Ovary inferior	**643**
615	Gynoecium apocarpous	**616**
	Gynoecium syncarpous or carpel 1	**620**
616	Leaves alternate	**617**
	Leaves opposite	**Monimiaceae**
617	Perianth segments 5	**618**
	Perianth segments 6	**Menispermaceae**
618	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**619**
619	Ovules 1 per carpel	**Phytolaccaceae**
	Ovules 2 or more per carpel	**Sterculiaceae**
620	Leaves alternate, radical, or absent	**621**
	Leaves opposite	**640**
621	Climbers	**622**
	Non-climbers	**624**
622	Styles 3, free	**Amaranthaceae**
	Styles connate or united, stigmas 3	**623**
623	Stamens 2–5 in male flowers; plants monoecious	**Euphorbiaceae**
	Stamens about 8 in male flowers; plants usually dioecious	**Polygonaceae**
624	Perianth segments 5, or perianth obscurely lobed or truncate	**625**
	Perianth segments 6	**637**
625	Leaves simple or absent	**626**
	Leaves compound	**635**
626	Perianth shallow cup shaped, scarcely lobed; stamens more or less sessile	**Gyrostemonaceae**
	Perianth more or less erect, clearly lobed; stamens with filaments	**627**
627	(1) Style and stigma 1	**628**
	(2) Styles or stigmas usually 2 or 3	**630**
	(3) Styles or stigmas 8 or more	**Phytolaccaceae**

628	Ovary 1–locular	629
	Ovary 3– or more–locular	**Sapindaceae**
629	Style terminal; ovule 1	**Euphorbiaceae**
	Style gynobasic; ovules 2	**Surianaceae**
630	Herbs	631
	Shrubs or trees	632
631	Ovary 1–locular	**Amaranthaceae**
	Ovary 2– or more–locular	**Euphorbiaceae**
632	Ovary 1–locular with 1 ovule	633
	Ovary 2–3–locular	**Euphorbiaceae**
633	Leaf base sheathing	**Polygonaceae**
	Leaf base not sheathing	634
634	Leaves stipulate	**Ulmaceae**
	Leaves exstipulate	**Chenopodiaceae**
635	Herbs	**Rosaceae**
	Shrubs or trees	636
636	Leaves 3–folioliate	**Euphorbiaceae**
	Leaves pinnate	**Sapindaceae**
637	Slender creeping perennials	**Polygonaceae**
	Shrubs or trees	638
638	Perianth in 2 whorls each of 3 united segments	**Ebenaceae**
	Perianth segments usually all free	639
639	Perianth segments in 1 series; style 1, entire or shortly lobed	**Sapindaceae**
	Perianth segments usually in 2 series; styles usually 3, simple or divided	**Euphorbiaceae**
640	*(from 620)*	
	Style 1, with 1 or 2 stigmas	641
	Styles 2 or more	**Euphorbiaceae**
641	Woody climbers	**Nyctaginaceae**
	Shrubs or trees	642
642	Stamens 2 in male flowers	**Oleaceae**
	Stamens more than 2	**Sapindaceae**
643	*(from 614)*	
	Leaves compound	**Apiaceae**
	Leaves simple	644
644	(1) Style and stigma 1, or stigma sessile	**Combretaceae**
	(2) Styles or stigmas 2	645
	(3) Styles or stigmas 3–8	646
645	Fruit a cypsela	**Asteraceae**
	Fruit a schizocarp	**Apiaceae**

646	Fruit a nut	**Fagaceae**
	Fruit a capsule	**Datiscaceae**
647	*(from 572)*	
	Latex present	**648**
	Latex absent	**652**
648	(1) Ovary 3–locular, superior	**Euphorbiaceae**
	(2) Ovary 1–locular, inferior	**Asteraceae**
	(3) Ovary not as above	**649**
649	Perianth in 1 series of 4 or 5 segments	**651**
	Perianth in 2 series; sepals 2; petals 4	**650**
650	Ovary superior	**Papaveraceae**
	Ovary inferior	**Rubiaceae**
651	Stamens 4; trees	**Moraceae**
	Stamens indefinite; mostly herbs	**Papaveraceae**
652	Ovary or gynoecium superior	**653**
	Ovary inferior	**792**
653	Gynoecium apocarpous	**654**
	Gynoecium syncarpous or carpel 1	**667**
654	(1) Perianth segments 2	**Winteraceae**
	(2) Perianth segments 4	**655**
	(3) Perianth segments 5	**660**
	(4) Perianth segments 6	**662**
655	Climbers	**Ranunculaceae**
	Non-climbers	**656**
656	Herbs	**657**
	Shrubs or trees	**658**
657	Leaves radical	**Ranunculaceae**
	Leaves alternate	**Phytolaccaceae**
658	Perianth segments united	**Sterculiaceae**
	Perianth segments free	**659**
659	Leaves stipulate	**Magnoliaceae**
	Leaves exstipulate	**Monimiaceae**
660	Leaves gland-dotted	**Rutaceae**
	Leaves, if present, not gland-dotted	**661**
661	(1) Leaves all alternate, or absent	**Phytolaccaceae**
	(2) Leaves radical, or radical and alternate	**Ranunculaceae**
	(3) Leaves opposite	**Cunoniaceae**
662	(1) Leaves mostly radical	**663**
	(2) Leaves all alternate	**664**
	(3) Leaves opposite	**Monimiaceae**
663	Leaf pitchers present	**Cephalotaceae**
	Leaf pitchers absent	**Ranunculaceae**

664	(1) Aquatic herbs with peltate leaves	**Cabombaceae**
	(2) Woody climbers	**Menispermaceae**
	(3) Shrubs or trees, non-climbers	**665**
665	Stamens 8	**Phytolaccaceae**
	Stamens indefinite	**666**
666	Leaves distichous; receptacle short	**Annonaceae**
	Leaves not distichous; receptacle elongated	**Magnoliaceae**
667	*(from 653)*	
	(1) Perianth segment 1	**Caryophyllaceae**
	(2) Perianth segments 2	**668**
	(3) Perianth segments 3	**670**
	(4) Perianth segments 4	**674**
	(5) Perianth segments 5	**719**
	(6) Perianth segments 6	**771**
668	Stamens 5 or fewer	**Chenopodiaceae**
	Stamens indefinite	**669**
669	Herbs or small shrubs	**Papaveraceae**
	Trees	**Winteraceae**
670	(1) Leaves alternate	**671**
	(2) Leaves opposite or verticillate	**673**
	(3) Leaves absent	**Chenopodiaceae**
671	Style 1	**672**
	Styles 2 or 3	**Amaranthaceae**
672	Tendrils present	**Vitaceae**
	Tendrils absent	**Caryophyllaceae**
673	Stigma 1	**Lythraceae**
	Stigmas 3	**Elatinaceae**
674	Leaves alternate, radical, or absent	**675**
	Leaves opposite or verticillate	**708**
675	Style and stigma 1	**676**
	Styles or stigmas more than 1	**701**
676	(1) Stamens 2	**678**
	(2) Stamens 3	**Rosaceae**
	(3) Stamens 3, staminode 1	**Proteaceae**
	(4) Stamens 4	**682**
	(5) Stamens 5	**Rosaceae**
	(6) Stamens 6	**677**
	(7) Stamens more than 6	**695**
677	Fruit a berry	**Lauraceae**
	Fruit an achene	**Rosaceae**
678	Leaves simple or absent	**679**
	Leaves compound	**681**

679	Leaves radical or absent	**Lentibulariaceae**
	Leaves alternate	**680**
680	Herbs; perianth segments free	**Brassicaceae**
	Shrubs; perianth segments united	**Thymelaeaceae**
681	Floating aquatics	**Lentibulariaceae**
	Rooted land plants	**Rosaceae**
682	Plants usually climbers with leaf-opposed tendrils	**Vitaceae**
	Plants without tendrils	**683**
683	Leaves compound	**684**
	Leaves simple	**686**
684	Stamens epiphyllous	**Proteaceae**
	Stamens not epiphyllous	**685**
685	Fruit an achene	**Rosaceae**
	Fruit a legume	**Caesalpiniaceae**
686	Leaves with stinging hairs	**Urticaceae**
	Leaves without stinging hairs	**687**
687	Stamens distinctly epiphyllous	**688**
	Stamens adhering to base of perianth, or free from it	**689**
688	Stamens same number as and opposite perianth segments and often sessile on them	**Proteaceae**
	Stamens same number as and alternate with perianth segments, or twice as many	**Elaeagnaceae**
689	Flowers in axillary spikes	**690**
	Flowers not in spikes	**692**
690	Leaves glabrous or with scattered hairs	**691**
	Underside of leaves white with close-set hairs	**Urticaceae**
691	Perianth segments united into 4–lobed floral tube	**Opiliaceae**
	Perianth segments not united	**Santalaceae**
692	Perianth petaloid	**693**
	Perianth sepaloid	**694**
693	Stamens same number as and opposite perianth segments	**Proteaceae**
	Stamens same number as and alternate with perianth segments, or more numerous	**Phytolaccaceae**
694	Flowers ebracteate, in terminal racemes	**Brassicaceae**
	Flowers bracteate, in clusters, cymes, or heads	**Urticaceae**
695	*(from 676)*	
	Leaves simple	**696**
	Leaves compound	**700**
696	Herbs	**697**
	Shrubs or trees	**698**

697	Sepals 2, valvate, completely enclosing bud; ovules several in each loculus	**Papaveraceae**
	Sepals not as above; ovule 1 in each loculus	**Phytolaccaceae**
698	Stamens 10 or fewer	**Thymelaeaceae**
	Stamens indefinite	**699**
699	Leaves gland-dotted	**Winteraceae**
	Leaves not gland-dotted	**Tiliaceae**
700	Shrubs or trees	**Caesalpiniaceae**
	Herbs	**Rosaceae**
701	*(from 675)*	
	(1) Stamens 4 or fewer	**702**
	(2) Stamens 5–10	**705**
	(3) Stamens indefinite	**707**
702	Herbs, either aquatic or growing in wet places; leaves radical, floating or absent; sepals 2; petals united, corolla 2–lipped	**Lentibulariaceae**
	Plants not as above	**703**
703	Leaves with ochrea	**Polygonaceae**
	Leaves without ochrea	**704**
704	Herbs or shrubs; leaves covered with mealy scales	**Chenopodiaceae**
	Trees	**Ulmaceae**
705	Style 1, stigmas usually 2	**Sapindaceae**
	Styles more than 1	**706**
706	Trees with irritant hairs; stipules reniform; fruit a large drupe	**Davidsoniaceae**
	Herbs without irritant hairs; stipules sheath-like; fruit a small nut	**Polygonaceae**
707	Ovary 3– to 5–locular	**Nymphaeaceae**
	Ovary 1–locular	**Papaveraceae**
708	*(from 674)*	
	Style and stigma 1	**709**
	Styles or stigmas more than 1	**716**
709	(1) Stamens 2	**710**
	(2) Stamens 3 or 5	**Lythraceae**
	(3) Stamens 4	**712**
	(4) Stamens 8	**Thymelaeaceae**
710	Stamens free from perianth, united into a cup at base	**Amaranthaceae**
	Stamens adnate to perianth	**711**
711	Annual herbs, frequently in moist situations	**Lythraceae**
	Small shrubs	**Thymelaeaceae**
712	Leaves with stinging hairs	**Urticaceae**
	Leaves without stinging hairs	**713**

713	Stamens distinctly adnate to perianth	**714**
	Stamens free from perianth or attached at the very base of the perianth segments	**715**
714	Shrubs or trees	**Proteaceae**
	Herbs	**Lythraceae**
715	Herbs	**Amaranthaceae**
	Shrubs or trees	**Santalaceae**
716	*(from 708)*	
	(1) Stamen 1	**Caryophyllaceae**
	(2) Stamens 4 alternating with the perianth lobes	**Aizoaceae**
	(3) Stamens 4, opposite the perianth lobes	**Santalaceae**
	(4) Stamens more than 4	**717**
717	Styles 2	**Cunoniaceae**
	Styles 4	**718**
718	Stamens indefinte	**Aizoaceae**
	Stamens 8	**Cunoniaceae**
719	*(from 667)*	
	Leaves alternate, radical, or absent	**720**
	Leaves opposite or verticillate	**757**
720	Stamens 5 or fewer	**721**
	Stamens more than 5	**740**
721	Style and stigma 1	**722**
	Styles or stigmas more than 1	**729**
722	Climbers with leaf-opposed tendrils	**Vitaceae**
	Non-climbers, or climbers without leaf-opposed tendrils	**723**
723	Leaves simple or absent	**724**
	Leaves compound	**Caesalpiniaceae**
724	Flowers in clusters of 2–4, surrounded by conspicuous coloured bracts	**Nyctaginaceae**
	Flowers not as above	**725**
725	(1) Stamens 2 or 3, with or without anthers, united at base into a short cup	**Amaranthaceae**
	(2) Stamens 3; staminodes 5	**Olacaceae**
	(3) Stamens 5, all with anthers	**726**
726	Herbs or undershrubs	**Amaranthaceae**
	Shrubs or trees	**727**
727	Stamens alternate with perianth segments	**728**
	Stamens opposite perianth segments	**Santalaceae**
728	Ovary surrounded by nectar-secreting disc	**Rhamnaceae**
	Ovary not surrounded by nectar-secreting disc	**Sterculiaceae**

729	(1) Tendril climbers	730
	(2) Twiners, without tendrils	731
	(3) Not climbers or twiners	732
730	Tendrils axillary	**Passifloraceae**
	Tendrils terminating inflorescence	**Polygonaceae**
731	Perianth segments free; styles 3	**Amaranthaceae**
	Perianth segments united; style 1, with 2 short stigmas	**Rhamnaceae**
732	Herbs	733
	Shrubs or trees	737
733	Ovary 1–locular, with 1–several ovules	735
	Ovary 3–5–locular, with several ovules in each loculus	734
734	Flowers hypogynous; calyx free, divided to base or nearly so	**Molluginaceae**
	Flowers perigynous; calyx entirely or partly adnate to ovary, or free but with a distinct tube	**Aizoaceae**
735	Leaves with ochrea	**Polygonaceae**
	Leaves without ochrea	736
736	Flowers with 1 bract and usually 1–2 bracteoles	**Amaranthaceae**
	Flowers without bracts or bracteoles	**Chenopodiaceae**
737	Stamens opposite perianth segments	738
	Stamens alternating with perianth segments	739
738	Perianth segments free; tall shrubs or trees	**Ulmaceae**
	Perianth segments united; shrubs, usually small	**Chenopodiaceae**
739	Stamens 5; staminodes 5; ovary 5–locular	**Sterculiaceae**
	Stamens 5; ovary 2– or 3–locular	**Rhamnaceae**
740	*(from 720)*	
	Leaves simple or absent	741
	Leaves compound	755
741	Style 1	742
	Styles 2 or more, free	752
742	Stigma large, peltate	**Surianaceae**
	Stigma not peltate	743
743	Flowers in clusters of 3–5, surrounded by 3 large coloured bracteoles	**Nyctaginaceae**
	Flowers not surrounded by conspicuous bracteoles	744
744	(1) Climbers	**Polygonaceae**
	(2) Herbs, non-climbers	745
	(3) Shrubs or trees	747
745	Stamens 10 or fewer	746
	Stamens indefinite	**Molluginaceae**

746	Flowers hypogynous	**Polygonaceae**
	Flowers perigynous	**Aizoaceae**
747	Perianth segments united	**748**
	Perianth segments free	**750**
748	Leaves absent; stems flat and green	**Polygonaceae**
	Leaves present	**749**
749	Stamens 10 or fewer; stigmas 2 or 3	**Sapindaceae**
	Stamens indefinite; stigma 1	**Elaeocarpaceae**
750	Flowers small, in heads or spikes; stamens exserted	**Mimosaceae**
	Flowers not in heads or spikes; stamens usually not exserted	**751**
751	Seeds endospermic; stipules present, often caducous	**Flacourtiaceae**
	Seeds non-endospermic; stipules absent	**Lauraceae**
752	(1) Styles 2	**Polygonaceae**
	(2) Styles 3	**753**
	(3) Styles 5	**Aizoaceae**
	(4) Styles about 8	**Phytolaccaceae**
753	Ovary 1–locular; ovule 1	**Polygonaceae**
	Ovary 3–locular; ovules several in each loculus	**754**
754	Flowers hypogynous; calyx free, divided to base or nearly so	**Molluginaceae**
	Flowers perigynous; calyx entirely or partly adnate to ovary, or free but with a distinct tube	**Aizoaceae**
755	*(from 740)*	
	(1) Leaves pinnate; stigma 1	**756**
	(2) Leaves pinnate; stigmas 2	**Sapindaceae**
	(3) Leaves bipinnate	**Mimosaceae**
756	Ovary 1–locular	**Caesalpiniaceae**
	Ovary 2– or more–locular	**Sapindaceae**
757	*(from 719)*	
	Style and stigma 1	**758**
	Styles or style-branches more than 1	**763**
758	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	**759**
759	Stamens free from perianth	**760**
	Stamens adnate to perianth	**761**
760	Perianth segments free	**Amaranthaceae**
	Perianth segments united	**Nyctaginaceae**
761	Opposite leaves unequal in size	**Aizoaceae**
	Opposite leaves equal in size	**762**
762	Stamens 10	**Thymelaeaceae**
	Stamens less than 10	**Lythraceae**

763	(1) Stamen 1	**Caryophyllaceae**
	(2) Stamens 2–5	**764**
	(3) Stamens more than 5	**768**
764	Stamens free from perianth	**765**
	Stamens adnate to perianth	**Aizoaceae**
765	Ovule 1	**767**
	Ovules more than 1	**766**
766	Placentation free-central	**Caryophyllaceae**
	Placentation axile	**Molluginaceae**
767	Perianth segments scarious	**Amaranthaceae**
	Perianth segments herbaceous	**Chenopodiaceae**
768	Flowers hypogynous	**769**
	Flowers perigynous; stamens borne on calyx-tube	**Aizoaceae**
769	Herbs	**770**
	Shrubs or trees	**Cunoniaceae**
770	Ovary 1–locular; leaves opposite or verticillate	**Caryophyllaceae**
	Ovary 3–5–locular; leaves alternate, often clustered in axils so as to appear verticillate	**Aizoaceae**
771	*(from 667)*	
	Leaves alternate, radical, or absent	**772**
	Leaves opposite or verticillate	**787**
772	Sepals 2, often caducous; petals 4	**773**
	Perianth in 1 series or, if in 2 series, usually of 3 + 3 segments	**774**
773	Flowers actinomorphic; stamens numerous	**Papaveraceae**
	Flowers zygomorphic; stamens 6	**Fumariaceae**
774	(1) Stamens 3	**775**
	(2) Stamens 5 or 6, sometimes with staminodes	**777**
	(3) Stamens more than 6	**781**
775	Trees or shrubs	**776**
	Climbers with leaf-opposed tendrils	**Vitaceae**
776	Style and stigma 1	**Lauraceae**
	Styles 2–3	**Euphorbiaceae**
777	Plants without tendrils	**778**
	Climbers with leaf-opposed tendrils	**Vitaceae**
778	Leaves large, compound	**Burseraceae**
	Leaves simple	**779**
779	Perianth segments free	**780**
	Perianth segments united	**Ebenaceae**
780	Leaves with ochrea	**Polygonaceae**
	Leaves without ochrea	**Euphorbiaceae**

781	Leafless parasitic twiners	**Lauraceae**
	Non-twiners	**782**
782	Style and stigma 1	**783**
	Styles or stigmas 2–3	**786**
783	Flowers with 1 or more long spurs	**Ranunculaceae**
	Flowers lacking spurs	**784**
784	Ovary 1–locular	**Lauraceae**
	Ovary 2– or more–locular	**785**
785	Leaves gland-dotted	**Rutaceae**
	Leaves not gland-dotted	**Elaeocarpaceae**
786	Perianth segments free	**Polygonaceae**
	Perianth segments united	**Ebenaceae**
787	*(from 771)*	
	(1) Stamens 3	**Elatinaceae**
	(2) Stamens 9, usually with 3 staminodes	**Lauraceae**
	(3) Stamens 10 or indefinite	**788**
788	Woody climbers	**Monimiaceae**
	Non-climbers	**789**
789	Leaves trifoliolate	**Cunoniaceae**
	Leaves not trifoliolate	**790**
790	Herbs	**Lythraceae**
	Shrubs or small trees	**791**
791	Carpels 2	**Aquifoliaceae**
	Carpels 4–15	**Sonneratiaceae**
792	*(from 652)*	
	Plants parasitic (mistletoes)	**Loranthaceae**
	Plants not parasitic	**793**
793	Leaves alternate, radical, or absent	**794**
	Leaves opposite or verticillate	**809**
794	Leaves gland-dotted	**795**
	Leaves not gland-dotted, or leaves absent	**796**
795	Stamens 10	**Combretaceae**
	Stamens indefinite	**Myrtaceae**
796	Perianth actinomorphic	**797**
	Perianth zygomorphic	**808**
797	(1) Perianth quite entire, or of 3 segments	**Aristolochiaceae**
	(2) Perianth segments 4	**798**
	(3) Perianth segments 5 or 6	**800**
798	(1) Stamens 2	**Gunneraceae**
	(2) Stamens 4	**799**
	(3) Stamens 5	**Asteraceae**
	(4) Stamens 6 or more	**Aizoaceae**

799	(1) Flowers in umbels	**Araliaceae**
	(2) Flowers in heads surrounded by involucral bracts	**Asteraceae**
	(3) Flowers not in umbels or heads	**Santalaceae**
800	Stamens 5	**801**
	Stamens more than 5	**806**
801	Anthers free	**802**
	Anthers united around style	**Asteraceae**
802	Herbs	**Apiaceae**
	Shrubs or trees	**803**
803	Style 1, with 1–2 stigmas	**804**
	Styles 2, free	**Araliaceae**
804	Stamens opposite perianth segments	**Santalaceae**
	Stamens alternating with perianth segments	**805**
805	Leaves simple and entire	**Rhamnaceae**
	Leaves compound or dissected	**Araliaceae**
806	Leaves simple	**807**
	Leaves compound	**Araliaceae**
807	Trees; stamens usually 10	**Combretaceae**
	Herbs or shrubs; stamens usually indefinite	**Aizoaceae**
808	*(from 796)*	
	Stigmas 1 or 2, each with indusium	**Goodeniaceae**
	Stigmas 3–6, without indusium	**Aristolochiaceae**
809	*(from 793)*	
	Leaves gland-dotted	**Myrtaceae**
	Leaves not gland-dotted	**810**
810	(1) Perianth segments 3	**Rubiaceae**
	(2) Perianth segments 4	**811**
	(3) Perianth segments 5	**816**
	(4) Perianth segments 6	**818**
811	(1) Stamens 2	**Thymelaeaceae**
	(2) Stamens 4; anthers not syngenesious	**813**
	(3) Stamens 4–5; anthers syngenesious	**Asteraceae**
	(4) Stamens 8	**Cunoniaceae**
	(5) Stamens indefinite	**812**
812	Leaves simple	**Myrtaceae**
	Leaves compound or unifoliolate	**Flacourtiaceae**
813	Aquatic herbs	**Haloragaceae**
	Plants not aquatic	**814**
814	Leaves opposite	**815**
	Leaves in whorls of 4–8	**Rubiaceae**
815	Stamens alternating with perianth segments	**Rubiaceae**
	Stamens opposite perianth segments	**Santalaceae**

816	(1) Stamens 1	**Valerianaceae**
	(2) Stamens 5	**817**
	(3) Stamens indefinite	**Aizoaceae**
817	(1) Anthers syngenesious	**Asteraceae**
	(2) Anthers free, opposite perianth segments	**Santalaceae**
	(3) Anthers free, alternating with perianth segments	**Rubiaceae**
818	Leaves simple	**819**
	Leaves compound	**Caprifoliaceae**
819	(1) Stamens 3	**Rubiaceae**
	(2) Stamens 10	**Portulacaceae**
	(3) Stamens indefinite	**Sonneratiaceae**
820	*(from 2)*	
	Latex present	**821**
	Latex absent	**822**
821	Styles or stigmas 3 or more	**Euphorbiaceae**
	Style or stigma 1	**Moraceae**
822	Succulent herbs 5–10 cm high, parasitic on roots; leaves absent or scale-like	**Balanophoraceae**
	Plants not parasitic; leaves green if present	**823**
823	Flowers mostly unisexual	**824**
	Flowers mostly bisexual	**836**
824	Climbers or twiners	**825**
	Non-climbers	**826**
825	Placentation apical	**Cannabaceae**
	Placentation basal	**Piperaceae**
826	Leaves alternate	**827**
	Leaves opposite	**828**
827	Leaves in whorls of 4 or more, or reduced to scales	**829**
	Leaves not as above	**830**
828	Aquatic herbs, usually non-littoral; seeds endospermic	**Callitrichaceae**
	Littoral shrubs; seeds non-endospermic	**Bataceae**
829	Shrubs or trees; leaves reduced to minute scales	**Casuarinaceae**
	Aquatic herbs; leaves entire or divided but not reduced to scales	**Haloragaceae**
830	Plants monoecious	**831**
	Plants dioecious	**833**
831	Herbs or undershrubs; flowers in heads	**Asteraceae**
	Trees; flowers otherwise	**832**
832	Leaves serrate-crenate; deciduous	**Betulaceae**
	Leaves entire; evergreen	**Euphorbiaceae**
833	Leaves not dissected	**834**
	Leaves palmately dissected	**Cannabaceae**

834	Both male and female flowers in dense spikes	**Salicaceae**
	Female flowers solitary or racemose; male flowers solitary or in spikes	**835**
835	Male flowers in catkins; female flowers with involucre of bracts but no perianth	**Balanopaceae**
	Male flowers solitary or in open spikes; perianth shallow cup-shaped, inconspicuous	**Gyrostemonaceae**
836	*(from 823)*	
	Herbaceous plants, growing only on rocks in running water	**Podostemaceae**
	Land plants	**837**
837	Stamens 10 or fewer, usually 2–3	**Piperaceae**
	Stamens indefinite	**Mimosaceae**

Monocotyledons

838	*(from 1)*	
	Plants of marine or brackish habitats	**839**
	Plants of fresh-water or land habitats	**845**
839	Leaves ligulate	**840**
	Leaves eligulate	**842**
840	Plants of brackish habitats	**Zannichelliaceae**
	Marine plants	**841**
841	Leaf blade and sheath shed leaving a circular scar	**Cymodoceaceae**
	Leaf blade shed but sheath persistent and fibrous	**Posidoniaceae**
842	Leaves with 1–5 longitudinal veins	**843**
	Leaves with 7 or more longitudinal veins	**Hydrocharitaceae**
843	Leaves 1–3 per shoot	**Hydrocharitaceae**
	Leaves 4 or more per shoot	**844**
844	Carpel solitary; stigmas 2, filiform	**Zosteraceae**
	Carpels 4–8; stigma 1, peltate	**Ruppiaceae**
845	Floating plants with one or more flat, leaf-like stems 1–8 mm in diameter, cohering by their edges, with or without roots hanging from the undersurface	**Lemnaceae**
	Plants not as above	**846**
846	Flowers unisexual	**847**
	Flowers bisexual	**869**
847	Leaves opposite or verticillate	**848**
	Leaves alternate, radical, crowded at apex of stem, or absent	**850**
848	Slender, twining land plants	**Dioscoreaceae**
	Aquatic or marsh plants	**849**

849	Perianth in male flowers absent or of one segment	**Najadaceae**
	Perianth segments in male flowers 3 + 3; stamens 3–9	**Hydrocharitaceae**
850	Leaves simple	**851**
	Leaves compound	**868**
851	Flowers closely packed in a dense, simple, unbranched spadix, with a usually convolute, coloured, or petal-like spathe arising from base	**Araceae**
	Spathe sometimes present, but inflorescence not as above and often branched	**852**
852	Trees or shrubs, rarely climbers; aerial stem woody	**853**
	Herbs (sometimes large, e.g. banana)	**854**
853	Perianth absent; trees, shrubs, or climbers	**Pandanaceae**
	Perianth segments 3 + 3; climbers	**Smilacaceae**
854	Flowers inconspicuous, often minute, within imbricate bracts or scales, in heads or spikelets; perianth absent or of 1–8 scales or bristles, usually concealed within bracts	**855**
	Flowers otherwise	**859**
855	Flowers small in spherical androgynous heads 2–8 mm in diameter without conspicuous bracts; mostly marsh or aquatic plants	**Eriocaulaceae**
	Flowers in spikelets surrounded by glume-like bracts	**856**
856	Leaf-sheath with free margins, sometimes overlapping	**857**
	Leaf-sheath with connate margins	**Cyperaceae**
857	Leaves ligulate	**Poaceae**
	Leaves eligulate	**858**
858	Wiry plants with jointed stems	**Restionaceae**
	Tiny, slender plants without erect stems	**Hydatellaceae**
859	Aquatic or marsh plants	**860**
	Land plants	**863**
860	Ovary inferior	**Hydrocharitaceae**
	Ovary superior	**861**
861	Plants dioecious	**Hanguanaceae**
	Plants monoecious	**862**
862	Flowers in cylindrical, terminal spikes	**Typhaceae**
	Flowers in globular, lateral heads	**Sparganiaceae**
863	Climbers	**864**
	Non-climbers	**865**
864	Ovary superior	**Smilacaceae**
	Ovary inferior	**Dioscoreaceae**
865	Ovary superior	**866**
	Ovary inferior	**Musaceae**

866	Leaves large, pinnately or palmately divided (palms)	**Arecaceae**
	Leaves otherwise	**867**
867	(1) Fruit containing many small seeds	**Juncaceae**
	(2) Fruit containing 3 large seeds	**Liliaceae**
	(3) Fruit a fleshy, thick-walled, 1–3-seeded drupe; leaves with many cross-nerves	**Hanguanaceae**
868	*(from 850)*	
	Ovary superior	**Arecaceae**
	Ovary inferior	**Dioscoreaceae**
869	*(from 846)*	
	Flowers closely packed in a simple spadix, usually with coloured spathe more or less enclosing it	**Araceae**
	Flowers not in spadix; inflorescence often branched; spathe sometimes present	**870**
870	Gynoecium apocarpous	**871**
	Gynoecium syncarpous or carpel 1	**877**
871	Land plants	**872**
	Aquatic or marsh plants	**874**
872	Woody plants; leaves compound, or pinnately or palmately divided (palms)	**Arecaceae**
	Small herbaceous plants; leaves, if present, entire	**873**
873	Saprophyte, lacking chlorophyll; leaves reduced to scales	**Triuridaceae**
	Tufted chlorophyllous herbs; leaves linear	**Centrolepidaceae**
874	(1) Perianth segments 2; stamens 6; carpels 3	**Aponogetonaceae**
	(2) Perianth segments 4; stamens 4; carpels 4	**Potamogetonaceae**
	(3) Perianth segments 3–6, rarely 4; stamens 3–indefinite; carpels 3–indefinite	**875**
875	Perianth segments all similar in texture and colour	**Juncaginaceae**
	The two perianth whorls different in texture and/or colour	**876**
876	Gynoecium of 3 or more free carpels; fruits achenes	**Alismataceae**
	Gynoecium of about 6 free carpels; fruits follicles	**Limnocharitaceae**
877	Ovary superior or perianth absent	**878**
	Ovary inferior	**909**
878	Flowers inconspicuous, often minute, within imbricate bracts or scales (glumes), in spikelets; perianth absent or of 1–8 scales or bristles, usually concealed within bracts	**879**
	Flowers otherwise	**883**
879	Leaves ligulate	**880**
	Leaves eligulate	**881**
880	Embryo visible through fruit wall	**Poaceae**
	Embryo not visible through fruit wall	**Cyperaceae**

881	Stamen 1	**882**
	Stamens more than one	**Cyperaceae**
882	Small annuals; inflorescence simple	**Centrolepidaceae**
	Rhizomatous perennials; inflorescence usually branched	**Cyperaceae**
883	Perianth segments 4 or fewer	**884**
	Perianth segments 6 (rarely 5)	**886**
884	(1) Stamen 1	**Philydraceae**
	(2) Stamens 3	**Xyridaceae**
	(3) Stamens 4	**885**
885	Leaves alternate; twiners	**Stemonaceae**
	Leaves radical; inflorescence spicate	**Araceae**
886	Leaves simple or absent	**887**
	Leaves compound (palms)	**Arecaceae**
887	Stems woody; leaves broad (palms)	**Arecaceae**
	Not as above	**888**
888	Stamens 3 (rarely 2)	**889**
	Stamens 6 (rarely 5)	**894**
889	Inner perianth segments free	**890**
	Inner perianth segments united	**Xyridaceae**
890	Perianth segments all similar in texture and colour	**891**
	The two perianth whorls different in texture and/or colour	**Commelinaceae**
891	Stamens free from perianth	**892**
	Stamens inserted at base of inner perianth segments	**Haemodoraceae**
892	Perianth segments petaloid	**Liliaceae**
	Perianth segments sepaloid	**893**
893	Carpels free or almost free; stigmas sessile	**Juncaginaceae**
	Carpels fused; style one, stigmas 3	**Juncaceae**
894	Leaf tips prolonged into tendrils	**895**
	Not as above	**896**
895	Corolla about 3 mm long	**Flagellariaceae**
	Corolla about 10 mm long	**Liliaceae**
896	Perianth segments all similar in texture and colour	**900**
	The two perianth whorls different in texture and/or colour	**897**
897	Much-branched leafy climbers	**Smilacaceae**
	Rosette or scrambling plants	**898**
898	Inflorescence spicate; glandular hairs present	**Commelinaceae**
	Flowers solitary or inflorescence cymose; if spicate no glandular hairs	**899**

899	Inner perianth segments fringed	**Liliaceae**
	Inner perianth segments not fringed	**Commelinaceae**
900	Perianth segments petaloid	**901**
	Perianth segments sepaloid	**905**
901	Aquatic plants, floating or rooted	**Pontederiaceae**
	Land plants	**902**
902	Coarse woody climbers; venation predominantly reticulate	**Smilacaceae**
	Non-climbers or, if climbers, the venation convergent	**903**
903	Inflorescence a tall woody spike	**Xanthorrhoeaceae**
	Inflorescence otherwise	**904**
904	Much-branched leafy climbers	**Smilacaceae**
	Not as above	**Liliaceae**
905	Marsh or aquatic plants	**Juncaginaceae**
	Land plants	**906**
906	Climbers	**Araceae**
	Non-climbers	**907**
907	Style 1, simple	**908**
	Style branched, stigmas 3	**Juncaceae**
908	Inflorescence a tall woody spike	**Xanthorrhoeaceae**
	Inflorescence otherwise	**Liliaceae**
909	*(from 877)*	
	(1) Flowers strongly gynandrous	**Orchidaceae**
	(2) Flowers only weakly gynandrous	**910**
	(3) Flowers not gynandrous	**911**
910	Venation pinnate	**Cannaceae**
	Venation convergent	**Orchidaceae**
911	Submerged aquatics; leaf lamina submerged or floating; styles or stigmas 6, each 2–lobed	**Hydrocharitaceae**
	Not as above	**912**
912	Leaves entire or with serrate margins	**913**
	Leaf lamina deeply dissected	**Taccaceae**
913	Climbing plants; leaves alternate with many longitudinal veins from midrib; veinlets reticulate	**Smilacaceae**
	Not as above	**914**
914	Venation obviously pinnate	**915**
	Venation convergent (middle vein sometimes stronger than others) parallel, or obscured by the thickness of leaf	**919**
915	Stamens 1–3	**916**
	Stamens 5	**Musaceae**

916	Ligule present at junction of leaf-sheath and lamina	**917**
	Leaves eligulate	**918**
917	Leaves 2–ranked	**Zingiberaceae**
	Leaves more than 2–ranked	**Costaceae**
918	Pulvinus present at junction of petiole (or leaf-sheath) and blade	**Marantaceae**
	Pulvinus absent	**Cannaceae**
919	Stamens 3	**920**
	Stamens 6	**923**
920	Perianth segments united at base	**921**
	Perianth segments free	**922**
921	Anthers with transverse dehiscence	**Burmanniaceae**
	Anthers with longitudinal dehiscence	**Iridaceae**
922	Ovules 1–2 per loculus	**Haemodoraceae**
	Ovules usually several per loculus	**Iridaceae**
923	Plant a colourless saprophyte	**924**
	Plant chlorophyllous	**925**
924	Perianth actinomorphic	**Burmanniaceae**
	Perianth zygomorphic	**Corsiaceae**
925	Leaf margins entire	**926**
	Leaf margins serrate	**Bromeliaceae**
926	Perianth segments all similar in texture and colour	**927**
	The two perianth whorls different in texture and/or colour	**Bromeliaceae**
927	Flowers in umbels, rarely solitary on a leafless scape	**Liliaceae**
	Flowers in simple or compound racemes	**928**
928	Leaves narrow, up to 20 cm long, arising from an underground rhizome	**Liliaceae**
	Leaves thick, fibrous, up to 2 m long, in tufts at base or apex of trunk-like stem	**Agavaceae**

GLOSSARY

Alison McCusker

This general glossary contains terms likely to be used frequently in the volumes of the *Flora* dealing with vascular plants. Specialised terms that are crucial to the understanding of individual family accounts, but not of wide application, will be explained and illustrated, where appropriate, in the relevant volumes.

Separate glossaries will be included in volumes dealing with the non-vascular groups (Volume 49ff.). However, where a word in the general glossary has a different application to non-vascular plants, its meaning in that context is included here.

It is the policy of the Editorial Committee to keep the use of technical terms within reasonable bounds so as to make it as easy as possible for the reader to consult the *Flora* without constant reference to the glossary. Simple explanations have been preferred to long and involved ones; the meanings given are believed to be accurate but are certainly not claimed to be complete. Words explained adequately, for botanical purposes, in *The Concise Oxford Dictionary* have generally not been included unless much more widely used in English in a different sense.

The glossary is also intended to guide the contributors to the *Flora*, who will number many before the project is completed, in the use of terminology. For that reason alternative spellings that are commonly used in the taxonomic literature are often not given.

abaxial: *of the side or surface of an organ*, facing away from the axis. cf. **adaxial.**

abscission: the normal shedding from a plant of an organ that is mature or aged, e.g. a ripe fruit, an old leaf. adj. **abscissile.**

accessory fruit: a fruit, or group of fruits derived from one flower, in which the conspicuous, fleshy portion develops from the receptacle and is shed with the true fruit(s) attached.

accumbent: *of the orientation of an embryo*, with the radicle lying against the edges of the two cotyledons.

achene: a dry, indehiscent fruit formed from a superior ovary of one carpel and containing one seed which is free from the pericarp (often applied, less correctly, to the one-seeded fruits of Asteraceae). cf. **cypsela.**

acicular: needle-shaped and stiff. Fig. 23.

aciculate: finely scored on the surface, as if scratched by a pin.

acropetal: arising or developing in a longitudinal sequence beginning at the base and proceeding towards the apex. cf. **basipetal.**

acrostichoid: *of sporangia*, densely covering the abaxial surface of the fertile frond, i.e. not in distinct groups; *of ferns*, having the sporangia arranged as above.

actinomorphic: *of flowers*, symmetrical about more than one vertical plane. cf. **zygomorphic.**

acuminate: tapering gradually to a protracted point. Fig. 23.

acute: terminating in a distinct but not protracted point, the converging edges separated by an angle less than 90 degrees. Fig. 23.

adaxial: facing towards the axis. cf. **abaxial.**

adnate: fused to an organ of a different kind, e.g. applied to a stamen fused to a petal.

adventitious: arising in abnormal positions, e.g. roots arising from the shoot system, buds arising elsewhere than in axils of leaves.

adventive: introduced recently, in particular since colonisation by man.

aerenchyma: tissue incorporating large, gas-filled spaces interspersed with the cells in a characteristic pattern.

aestivation: the arrangement of sepals and petals or their lobes in an unexpanded flower bud. cf. **vernation.** Fig. 25.

aggregate fruit: a cluster of fruits formed from the free carpels of one flower.

albumen: = **endosperm.**

allopatric: *of two or more species*, having different ranges of distribution. cf. **sympatric.**

alternate: *of leaves or other lateral organs*, borne singly at different heights on the axis; *of floral parts*, on a different radius, e.g. describing the position of stamens with respect to petals.

anastomosis: fusion to form a network e.g. of veins in a leaf blade.

anatropous: *of an ovule*, inverted so that the micropyle faces the placenta. Fig. 25.

androdioecious: having bisexual flowers and male flowers, on separate plants.

androecium: the stamens of one flower collectively.

androgynophore: a stalk bearing both the androecium and gynoecium of a flower above the level of insertion of the perianth.

androgynous: having male and female flowers in the same inflorescence.

androphore: a stalk bearing the androecium.

anemophilous: pollinated by wind.

angiosperm: a seed-bearing plant whose ovules, and hence seeds, develop within an enclosed ovary. cf. **gymnosperm.**

annual: a plant whose life span ends within one year after germination.

annular: arranged in or forming a ring.

annulus: a ring; *in ferns*, the elastic ring of cells, forming part of the sporangium wall, that initiates dehiscence.

anterior: *of floral organs*, on the side of the flower farthest from the axis. cf. **posterior.**

anther: the pollen-bearing part of a stamen. cf. **filament.**

antheridium: the fertile organ of a male gametophyte or the male organ of a bisexual gametophyte, in which male gametes are formed.

anthesis: the time of opening of a flower.

anthocarp: a false fruit consisting of the true fruit and the base of the perianth, as in Nyctaginaceae.

antrorse: directed forwards or upwards. cf. **retrorse.**

apetalous: without petals.

apical: *of a placenta*, at the top of the ovary. Fig. 25.

apiculate: terminating in a short, sharp, flexible point. Fig. 23.

apocarpous: *of a gynoecium*, consisting of two or more carpels which are free from one another or almost so.

apomict: a plant that produces viable seed without fertilisation.

appendage: a structure arising from the surface or extending beyond the tip of another structure.

appressed: pressed closely against but not united with.

aquatic: living in or on water for all or a substantial part of the life span (generally restricted to fresh/inland waters).

arborescent: resembling a tree (applied to non-woody plants attaining tree height and to shrubs tending to become tree-like in size). cf. **dendroid.**

areole: a space between the threads of a net; *in Cactaceae*, a cluster of hairs/spines/bristles borne at the node of a leafless stem; *in Mimosaceae (for example)*, a distinct, oblong or elliptical area on the face of a seed, bounded by a fine line. adj. **areolate.**

aril: a structure partly or wholly covering the testa of a seed and formed by expansion of the funicle. adj. **arillate.**

aristate: having a stiff, bristle-like awn or tip. Fig. 23.

aristulate: having a small awn.

article: a segment of a jointed stem or of a fruit with constrictions between the seeds.

articulate: jointed; having joints where separation may occur naturally; *of a stem*, having nodes.

ascending: growing erect after an oblique or semi-horizontal beginning.

asexual: not forming part of a cycle which involves fertilisation and meiosis.

attenuate: tapering gradually.

auricle: an ear-shaped appendage at the base of a leaf, leaflet or corolla lobe. adj. **auriculate**. Fig. 23.

autochthonous: *of the inhabitants of a region*, original; earliest known; (applied to an element of the Australian flora rich in endemics and believed to have been evolving in Australia for a long period of time).

autotrophic: independent of other organisms in respect of organic nutrition; able to fix carbon dioxide, by photosynthesis, to form carbohydrates.

awn: a bristle-like appendage, e.g. on the tip or back of the lemma of a grass floret.

axil: the angle between a leaf or bract and the axis bearing it. adj. **axillary.**

axile: on an axis; *of a placenta*, on the central axis of the ovary. Fig. 25.

axis: a stem, (commonly used for the main stem of a whole plant or of an inflorescence).

barbellae: short, straight, stiff hairs or barbs.

basal: at the base; *of a placenta*, at the base of the ovary. Fig. 25.

basifixed: attached at or by the base, e.g. *of anthers*, by the base of the connective.

basipetal: developing, in sequence, from the apex towards the base. cf. **acropetal.**

basiscopic: pointing towards the base (applied to the first lateral vein of a leaflet on the side nearer the leaf base).

beak: a prominent terminal projection, especially of a carpel or fruit.

berry: a fleshy or pulpy indehiscent fruit with the seed(s) embedded in the fleshy tissue of the pericarp. cf. **drupe.**

biennial: a plant whose life span extends for more than one but less than two years after germination.

bifid: divided, for about half the length, into two parts. cf. **bipartite.**

bifoliate: *of plants*, having two leaves.

bifoliolate: *of leaves*, having two leaflets.

bilabiate: two-lipped, e.g. of a corolla in which fusion of an anterior group and a posterior group of petals extends beyond the top of the corolla tube.

bilocular: having two cavities.

bipartite: divided, nearly to the base, into two parts. cf. **bifid.**

bipinnate: *of leaves*, twice pinnately divided. Fig. 24.

biseriate: arranged in two rows or whorls.

bisexual: bearing both male and female organs together, e.g. on the same gametophyte or in the same flower.

blade: the expanded part of a leaf or petal.

bole: the trunk of a tree, below the lowest branch. cf. **canopy.**

bract: a leaf-like structure, different in form from the foliage leaves and without an axillary bud, associated with an inflorescence or flower.

bracteole: a small bract-like structure borne singly or in pairs on the pedicel or calyx of a flower.

bulb: a storage organ, usually underground, made up of a stem and leaf bases, the food reserves being stored in the inner, fleshy leaf bases.

bulbel: a bulb arising from another bulb.

bulbil: a small, deciduous bulb (or tuber) formed in the axil of a leaf and functioning to propagate the plant vegetatively.

burr: a rough or prickly propagule consisting of a seed or fruit and associated floral parts or bracts.

buttress: a flange of tissue protruding from the main outline of the base of a tree.

caducous: falling off early.

caespitose: growing in tufts.

callus: a protruding mass of hardened tissue, often formed after an injury but sometimes a regular feature of the plant, e.g. on the labellum of some orchids and the axis of the spikelet of some grasses. adj. **callose.**

calyptra: *in mosses*, a cap-like structure covering or partly covering the capsule and derived from the neck of the archegonium; *in a flower*, (= **operculum**), a cap covering the stamens and carpels in the bud and formed by fusion or cohesion of perianth parts.

calyx: the sepals of one flower collectively.

calyx-tube: a tube formed by fusion or cohesion of sepals. cf. **hypanthium.**

campanulate: bell-shaped.

campylotropous: *of an ovule*, orientated transversely, i.e. with its axis at right angles to its stalk, and with a curved embryo sac. Fig. 25.

canopy: the branches and foliage of a tree. cf. **bole.**

capitate: *of an inflorescence*, with the flowers unstalked and aggregated into a dense cluster; *of a stigma*, globose, like the head of a pin.

capitulum: a dense cluster of sessile flowers.

capsule: a dry fruit formed from two or more united carpels and dehiscing at maturity to release the seeds.

carpel: an organ (generally believed to be a modified foliar unit) at the centre of a flower, bearing one or more ovules and having its margins fused together or with other carpels to enclose the ovule(s) in an ovary, and consisting also of a stigma and usually a style.

carpophore: *in ferns*, the stalk of a sporocarp; *in a fruit*, the stalk of a mericarp.

caruncle (= strophiole): an outgrowth of a seed coat, near the hilum.

caryopsis: a dry, indehiscent, one-seeded fruit in which the seed coat is closely fused to the fruit wall (characteristic of grasses).

cataphyll: a scale leaf associated with a vegetative part of a plant, e.g. rhizome, perennating bud.

catkin: a spike in which the flowers are unisexual and without conspicuous perianth.

caudate: having a narrow tail-like appendage. Fig. 23.

caudex: a thick, erect trunk, especially of cycads.

caudicle: a thread to which a pollen mass is attached in Orchidaceae and Asclepiadaceae.

cauliflorous: see **cauline.**

cauline: *of leaves*, borne on an aerial stem; *of flowers or fruits*, borne on old wood (= **cauliflorous**).

cell: the basic unit of plant structure consisting, at least when young, of a protoplast surrounded by a wall.

centrifugal: directed, or developing, from the centre or axis outwards.

centripetal: directed, or developing, from the outside towards the centre or axis.

chaff: thin, membranous scales or bracts; thin, dry unfertilised ovules among the fully developed seeds of a fruit.

chalaza: the part of an ovule to which the end of the stalk (funicle) is attached.

chlorophyll: pigment(s) constituting the green colouring matter of plants and absorbing radiant energy in photosynthesis.

chromosome: a thread-like structure in the nucleus of a cell, containing a linear sequence of genes.

cilia: *in unicellular plants, gametes, spores etc.*, minute hair-like protoplasmic protrusions whose movement confers motility on the cell; *in higher plants*, hairs more or less confined to the margins of an organ. sing. **cilium**; adj. **ciliate.**

cincinnus: a spirally curled cymose inflorescence.

circinnate (= circinate): spirally coiled, with the tip innermost.

circumsciss: (to) break open along a transverse line around the circumference. adj. **circumscissile.**

cladode: the photosynthetic stem of a plant whose foliage leaves are absent or much reduced. cf. **phyllode.**

cladophyll: a flattened, leaf-like photosynthetic stem not bearing leaves or scales. cf. **phylloclade.**

class: a major taxonomic rank, between **order** and **division.**

clavate: club-shaped.

claw: a narrow, stalk-like basal portion of a petal, sepal or bract.

cleistogamous: *of flowers*, self-pollinating and setting fertile seed but never opening.

clone: a set of organisms produced from one parent by vegetative reproduction.

coccus: one of the (usually 1-seeded) lobes of a distinctly lobed fruit, becoming separate at maturity. pl. **cocci.**

cochlear: *of the arrangement of corolla lobes in a bud*, a variant of imbricate aestivation. Fig. 25.

cochleate: coiled like a snail-shell.

cohesion: the sticking together of floral parts of the same whorl without organic fusion. adj. **coherent.**

collateral: situated side by side; adjacent and on the same radius of an axis.

columella: the central axis of a moss capsule; *sometimes applied to* the central axis of fruits and cones.

column: the lower part of an awn in grasses, when distinctly different in form from the upper part; (=**gynostemium**), a structure in Orchidaceae, Asclepiadaceae and Stylidiaceae, extending above the ovary of a flower and incorporating stigma, style and stamens.

coma: a tuft of hairs. adj. **comose.**

commissure: a join or seam; the interfacing of two fused carpels in an ovary.

compound: *of a leaf*, having the blade divided into two or more distinct leaflets; *of an inflorescence*, made up of an aggregate of smaller inflorescences.

compressed: flattened in one plane, either dorsally (bringing the front and back closer together) or laterally (bringing the sides closer together).

conduplicate: folded together, with the fold-line along the long axis (e.g. *of cotyledons in a seed*).

cone: *in gymnosperms and club-mosses*, a group of sporophylls arranged compactly on a central axis; (loosely) *in Casuarina*, a woody multiple fruit incorporating the bracts and bracteoles associated with the flowers.

connate: fused to another organ (or other organs) of the same kind.

connective: the part of an anther that connects the lobes.

connivent: coming into contact; converging.

contorted: see **convolute.**

convolute: *of the arrangement of corolla lobes in a bud*, a form of imbricate aestivation in which each segment has one edge overlapping the adjacent segment, like a furled umbrella. Fig. 25.

cordate: *of a leaf blade*, broad and notched at the base; heart-shaped. Fig. 23.

corm: a fleshy, swollen stem base, usually underground, in which food reserves are stored between growing seasons.

corolla: the petals of a flower collectively.

corona: a ring of tissue arising from the corolla or perianth of a flower and standing between the perianth lobes and the stamens.

cortex: the region of a stem or root surrounding the vascular cylinder but inside the epidermis.

corymb: a racemose inflorescence in which the pedicels of the lower flowers are longer than those of the flowers above, bringing all flowers to about the same level.

cotyledon: the primary leaf (or one of two or more primary leaves) of an embryo.

crenate: with small, rounded teeth; scalloped. Fig. 24.

crenulate: minutely scalloped. Fig. 24.

crown: the part of a tree or shrub above the level of the lowest branch.

crustaceous: brittle; *of marine algae*, encrusted with calcium carbonate.

cryptogam: (literally) a plant whose sexual reproductive parts are not conspicuous; a plant that produces spores, not seeds, in its sexual reproductive cycle, e.g. ferns, mosses, algae. cf. **phanerogam.**

culm: an aerial stem, in grasses, sedges, rushes, etc., bearing the inflorescence.

cuneate: wedge-shaped. Fig. 23.

cuspidate: tapering into a sharp, rigid point. Fig. 23.

cyathium: an inflorescence of unisexual flowers surrounded by involucral bracts, as in *Euphorbia*.

cyclic: *of floral organs*, several borne at the same level on the axis; whorled. cf. **spiral.**

cyme: an inflorescence in which each flower, in turn, is formed at the tip of a growing axis and further flowers are formed on branches arising below it.

cypsela: a dry, indehiscent, one-seeded fruit formed from an inferior ovary.

cystolith: a stalked structure growing from a cell wall into the cell cavity, encrusted with calcium carbonate.

deciduous: falling seasonally, e.g. of the leaves or bark of some trees.

decompound: more than once compound.

decumbent: spreading horizontally but then growing upwards.

decurrent: extending downwards beyond the point of insertion, e.g. of a lamina extending downwards to form a flange along the petiole.

decussate: in pairs, with successive pairs borne at right angles to each other.

definite: of a constant number; *of stamens*, twice as many as the petals or sepals, or less; *of an inflorescence*, ending in a flower or an aborted floral bud.

deflexed: bent downwards.

dehiscent: breaking open at maturity to release the contents.

deltoid: triangular with the sides of about equal length. Fig. 23.

dendroid: tree-like in form but not in size.

dentate: toothed. Fig. 24.

denticulate: finely toothed. Fig. 24.

depressed: flattened as if pressed down from the top or end.

determinate: *of growth or branching*, with a bud or flower terminating the growth of the main axis; *of an inflorescence*, see **definite.**

diadelphous: having the stamens united into two groups, or all but one united in a group and one free.

dichasium: a cymose inflorescence with opposite branching below the flower which terminates each axis. cf. **monochasium.**

dichotomous: forking into two equal branches resulting from division of the growing point.

diclinous: having the stamens and the carpels in separate flowers.

dicotyledon: a flowering plant whose embryo has two (rarely more) cotyledons (seed leaves). cf. **monocotyledon.**

didymous: borne in pairs; *of anthers*, having two lobes, with scarcely any tissue connecting them.

didynamous: *of stamens*, four in number, two being distinctly longer than the other two.

digitate: branching from the axis or stalk like the fingers of a hand. Fig. 24.

dimorphic: of two different forms.

dioecious: having the male and female reproductive structures on separate plants. cf. **monoecious.**

diploid: having two of the basic sets of chromosomes in the nucleus. cf. **haploid, polyploid.**

disc: a plate or rim of tissue, derived from the receptacle of a flower, occurring between whorls of floral parts.

dissepiment: a partition (septum) within an ovary or fruit, derived by fusion of adjacent carpels.

distal: remote from the point of origin or attachment. cf. **proximal.**

distichous: arranged in two rows on opposite sides of a stem and thus in the same plane.

diurnal: *of flowers*, opening only during daylight hours.

divaricate: widely spreading.

division: the major taxonomic rank within the Plant Kingdom (in which the phylum is no longer generally recognised).

dorsal: *of a lateral organ*, (relating to the side) facing away from the axis, i.e. the 'back'; *of a thallus*, facing away from the substratum. cf. **ventral.**

dorsifixed: attached at or by the back.

dorsiventral: having structurally different upper and lower surfaces.

drupe: a succulent fruit formed from one carpel, having the seed(s) enclosed in an inner stony layer of the fruit wall. adj. **drupaceous** (which is often used to mean drupe-like but not strictly a drupe).

echinate: bearing stiff, stout, prickly hairs.

edaphic: pertaining to the soil.

elater: an elongated, spirally thickened, hygroscopic cell in the capsule of a liverwort, derived from sporogenous tissue and assisting in spore dispersal; an appendage to the spore of *Equisetum*.

elliptic: oval in outline, widest at the centre. Fig. 23.

emarginate: having a broad, shallow notch at the apex. Fig. 23.

embryo: a young plant contained within an archegonium or seed.

enation: an epidermal outgrowth.

endemic: having a natural distribution confined to a particular geographical region.

endocarp: the innermost layer of the wall of a fruit; *in a drupe*, the stony layer surrounding the seed.

endosperm: nutritive tissue in a seed, in angiosperms triploid and formed in the embryo sac after fertilisation, in gymnosperms haploid and derived from the sterile portion of the female gametophyte.

entire: having a smooth margin, not dissected or toothed. Fig. 24.

entomophilous: pollinated by insects.

ephemeral: short-lived.

epicalyx: a whorl of bracts, just below a flower, looking like a second calyx.

epicarp: the outer layer of the wall of a fruit, i.e. the 'skin'.

epicormic: *of buds, shoots or flowers*, borne on the old wood of trees (applied especially to shoots arising from dormant buds after injury or fire).

epidermis: the outermost layer of cells of an organ, usually only one cell thick.

epigeal: *of germination*, having the cotyledon(s) emerging from the seed coat and becoming photosynthetic. cf. **hypogeal.**

epigynous: *of floral parts (especially stamens)*, attached above the level of insertion of the ovary, and arising from tissue that is fused to the ovary wall. cf. **hypogynous, perigynous**. Fig. 26.

epipetalous: borne on the petals. Fig. 26.

epiphyllous: growing on leaves, e.g. applied to vegetatively propagated plantlets in some Crassulaceae.

epiphyte: a plant growing on, but not parasitic on, another plant (often loosely applied to plants, such as orchids, that grow on vertical rock faces).

eremean: pertaining to regions of low, irregular rainfall.

eusporangiate: *of ferns*, having sporangia with walls more than one cell thick. cf. **leptosporangiate.**

evergreen: bearing green leaves throughout the year.

exine: the outer layer of the wall of a pollen grain or spore.

exserted: protruding, e.g. of stamens with respect to a corolla tube.

exstipulate: without stipules.

extra-floral: *of nectaries*, not within the flower.

extrorse: *of anthers*, opening away from the centre of the flower.

facultative: *of parasites*, optional. cf. **obligate.**

falcate: sickle-shaped. Fig. 23.

family: a group of one to many genera believed to be related phylogenetically, usually clearly separable from other such groups.

farinaceous: containing starch grains; mealy; resembling flour.

fascicle: a cluster, adj. **fasciculate.**

fenestrate: having openings or translucent areas ('windows').

fertilisation: the union of male and female gametes.

filament: the stalk of a stamen; a thread one or more cells thick; *in blue-green Algae*, a trichome enclosed in a mucilaginous sheath.

filiform: thread-like. Fig. 23.

fistular: hollow throughout its length.

flaccid: limp; tending to wilt. cf. **turgid.**

flexuous (= flexuose): bent from side to side in a zig-zag form.

floral: belonging to or associated with a flower.

floret: a grass flower, together with the lemma and palea that enclose it (often applied to flowers in Cyperaceeae and Asteraceae).

flower: the sexual reproductive structure of the angiosperms, typically consisting of gynoecium, androecium and perianth and the axis bearing these parts.

foliaceous: leaf-like.

follicle: a dry, dehiscent fruit formed from one carpel and dehiscing along the line of fusion of its edges.

forb: a non-woody plant other than a grass, sedge, rush, etc. cf. **herb.**

free: not fused or united (with other organs).

free-central: a placentation in which the ovules are borne on a free-standing central placenta within the ovary. Fig. 25.

frond: a leaf especially of a fern, cycad or palm; a leaf-like portion of a non-vascular plant (e.g. a foliose alga).

fruit: the seed-bearing structure in angiosperms formed from the ovary after flowering.

frutescent: becoming shrub-like (woody).

fruticose: shrub-like.

fugacious: falling or withering away very early.

funicle (= funiculus): the stalk of an ovule.

fusiform: spindle-shaped, i.e. narrower at both ends than at the centre.

gamete: a cell or nucleus that fuses with another, of opposite sex, in sexual reproduction.

gametophyte: a plant, or phase of a plant's life cycle, that bears gametes.

gamopetalous (= sympetalous): with the petals united by their margins, at least at the base.

gamophyllous: having the leaves or perianth segments united by their margins, at least at the base.

gamosepalous: having the sepals united by their margins, at least at the base.

geniculate: bent abruptly like a knee joint.

genotype: the total complement of hereditary factors (genes) acquired by an organism from its parents and available for transmission to its offspring. cf. **phenotype.**

genus: a group of species believed to be related phylogenetically and usually clearly separable from other such groups, or a single species without close relatives. pl. **genera.**

geophyte: a plant whose perennating buds are buried in the soil.

glabrescent: becoming glabrous.

glabrous: without hairs.

gland: a structure, within or on the surface of a plant, with a secretory function.

glandular: bearing glands; functioning as a gland.

glaucous: blue-green in colour, with a whitish bloom (as in the juvenile leaves of many eucalypts).

globose: nearly spherical.

glomerule: a small compact cluster. adj. **glomerulate.**

glumaceous: glume-like, tending to be chaffy or membranous in texture.

glume: a bract in the inflorescence of a grass, sedge or similar plant.

grain: a fruit characteristic of grasses (= **caryopsis**); **pollen grain**, a microspore of a seed plant, or the partially developed gametophyte formed from it.

gymnosperm: a seed plant with the ovules borne on the surface of a sporophyll. cf. **angiosperm.**

gynobasic: *of a style*, arising near the base of the gynoecium, e.g. between the lobes of the ovary.

gynodioecious: having bisexual flowers and female flowers, on separate plants.

gynoecium: the carpels of a flower collectively.

gynophore: a stalk bearing the gynoecium above the level of insertion of the other floral parts.

gynostemium: see **column.**

habit: the growth form of a plant, comprising its size, shape, texture and orientation.

habitat: the environment in which a plant lives.

half-inferior: *of an ovary*, partly below and partly above the level of attachment of the perianth and stamens. Fig. 26.

halophyte: a plant adapted to living in highly saline habitats; a plant that accumulates high concentrations of salt in its tissues.

haploid: having a single set of chromosomes in the nucleus (i.e. having each gene locus represented only once).

hastate: spear-shaped; *of a leaf blade*, narrow and pointed but with two basal lobes spreading approximately at right angles. Fig. 23.

haustorium: an absorbing organ through which a parasite obtains chemical substances from its host.

helicoid: coiled; *of a cymose inflorescence*, branching repeatedly on the same side.

herb: any vascular plant that never produces a woody stem. cf. **forb.**

herbaceous: not woody; soft in texture.

hermaphrodite: = **bisexual.**

heterogamous: producing flowers of two or more kinds with respect to their fertile organs, e.g. male and female or bisexual and female. cf. **homogamous.**

heteromorphous (= heteromorphic): of two or more distinct forms.

heterosporous: producing separate male and female spores. cf. **homosporous.**

hilum: the scar on a seed coat at the place where it was attached to its stalk during development.

hirsute: bearing coarse, rough, longish hairs. cf. **villous.**

hispid: bearing stiff, bristly hairs.

hoary: covered with a greyish layer of very short, closely interwoven hairs.

holotype: a single specimen designated by the author of a plant (or animal) name, at the time of original publication, as that to which the name shall apply; the 'voucher specimen' of a name.

homogamous: having flowers of only one kind. cf. **heterogamous.**

homosporous: producing only one kind of spore in the sexual reproductive cycle, and hence one gametophyte which produces both male and female gametes. cf. **heterosporous.**

host: an organism on which a parasite lives and by which it is nourished (also applied, loosely, to a plant supporting an epiphyte).

hyaline: translucent, almost like clear glass.

hybrid: an offspring of genetically different parents (in a Flora, usually applied where the parents are of different species).

hygroscopic: absorbing water and undergoing movements or changes brought about by changes in water content.

hypanthium: a cup or tube bearing floral parts above the base, and often above the top, of the ovary of a flower, e.g. in many Myrtales.

hypocotyl: the part of the stem of an embryo or young seedling below the cotyledonary node.

hypogeal: *of germination*, having the cotyledon(s) remaining within the seed coat. cf. **epigeal.**

hypogynous: arising below the level of insertion of the ovary (often applied, loosely, to a *flower* in which the sepals, petals and stamens are inserted below the ovary). cf. **perigynous, epigynous**. Fig. 26.

imbricate: *of perianth parts*, having the edges overlapping in the bud. Fig. 25.

imparipinnate: having an uneven number of pinnae, by virtue of having one terminal pinna. cf. **paripinnate**. Fig. 24.

incised: cut deeply, sharply and often irregularly (an intermediate condition between toothed and lobed). Fig. 24.

included: enclosed, not protruding.

incumbent: *of the orientation of an embryo*, with the cotyledons lying face to face and folded downwards beside the radicle; *of anthers*, lying against the inner face of the filament.

incurved: bent or curved inwards or upwards; of *leaf margins*, curved towards the adaxial surface.

indefinite: variable in number; numerous; *of stamens*, more than twice as many as the petals or sepals; *of an inflorescence*, not terminating in a flower (i.e. having a continuing, terminal growing point).

indehiscent: not opening at maturity.

indeterminate (= monopodial): *of growth*, the condition in which the terminal bud persists and produces successive lateral branches.

indumentum: the epidermal appendages, e.g. hairs or scales, collectively.

induplicate: folded inwards so that the outer faces of the margins are in contact.

indusium: tissue covering the sorus of a fern; the pollen-cup of Goodeniaceae.

inferior: *of an ovary*, at least partly below the level of attachment of the other floral parts. cf. **superior**. Fig. 26.

inflexed: bent sharply upwards or forwards.

inflorescence: the group or arrangement in which flowers are borne on a plant.

infraspecific: of lower taxonomic rank than species.

insectivorous: catching, and ostensibly feeding on, insects.

inserted (*on*): attached to; arising from.

integument: a covering; one of the outer layers of tissue of an ovule.

internode: the portion of a stem between the level of insertion of two successive leaves or leaf pairs (or branches of an inflorescence).

interpetiolar: *of stipules*, between the petioles of two opposite leaves. cf. **intrapetiolar.**

interrupted: *of an inflorescence*, having the flowers unevenly distributed along the axis, with conspicuous gaps.

intramarginal: situated inside but close to the margin, e.g. of a vein in a leaf.

intrapetiolar: between a petiole and the subtending stem. cf. **interpetiolar.**

introduced: not indigenous; not native to the area in which it now occurs. cf. **adventive.**

introrse: of anthers, dehiscing towards the centre of the flower.

involucre: a group of bracts enveloping a condensed inflorescence; a layer of tissue enveloping particular structures, e.g. an archegonium in Bryophyta, sporangia in Hymenophyllaceae.

involute: rolled inwards; *of a leaf*, with the margins rolled towards the adaxial surface.

irregular: see **zygomorphic.**

isolateral (=isobilateral): having structurally similar upper and lower surfaces.

isotype: a specimen which is, or is believed to be, a duplicate of the holotype, i.e. part of the same collection.

juvenile: *of leaves*, formed on a young plant and different in form from the adult leaves.

karyoevolution: evolutionary change in the chromosome set, expressed as changes in number and gross structure of the chromosomes; (more broadly), evolutionary relationships between taxa as indicated by karyotype differences.

karyotype: the gross morphology of the chromosome set, described in terms of number, length, centromere position, etc.

keel: a ridge like the keel of a boat; *in particular*, a boat-shaped structure formed by fusion of the two anterior petals of a flower in Fabaceae.

keeled: *of leaves or bracts*, folded and ridged along the midrib.

labellum: a lip; *in Orchidaceae*, the distinctive median petal that serves as an alighting platform for pollinating insects.

laciniate: slashed into narrow, pointed lobes. Fig. 24.

lacuna: a gap or cavity.

lamella: a thin, plate-like layer; **middle lamella**, the layer between the walls of two adjacent cells.

lamina: the blade of a leaf.

lanceolate: *of a leaf*, about four times as long as it is broad, broadest in the lower half and tapering towards the tip. Fig. 23.

latex: a viscous fluid exuded from the cut surfaces of the leaves and stems of certain plants.

leaflet: one of the ultimate segments of a compound leaf.

lectotype: a specimen selected from among those cited with the original description to serve in place of a holotype where the holotype is missing or destroyed, or where no holotype was designated.

legume: a fruit characteristic of the families Mimosaceae, Caesalpiniaceae and Fabaceae, formed from one carpel and either dehiscent along both sides, or indehiscent; *in particular*, such a fruit that is grown as an edible crop; a crop species in the family Fabaceae.

lemma: the lower of two bracts enclosing a grass flower.

lenticel: a loosely-packed mass of cells in the bark of a woody plant, visible on the surface of a stem as a raised powdery spot, through which gaseous exchange occurs.

lenticular: shaped like a biconvex lens.

lepidote: covered with small, membranous scales.

leptosporangiate: *of ferns*, having sporangia with walls only one cell thick. cf. **eu–sporangiate.**

liane: a climbing or twining plant (usually applied to woody climbers).

lignotuber: a woody swelling below or just above the ground, containing adventitious buds from which new shoots develop if the top of the plant is cut or burnt (common in the shrubby eucalypts and in many other fire-tolerant Australian shrubs).

ligulate: bearing a ligule; strap-shaped.

ligule: a strap-shaped structure; a membranous or hairy appendage on the adaxial surface of a leaf, especially in grasses, at the junction between sheath and blade; a small adaxial appendage near the leaf base in some pteridophytes; the corolla limb in ray flowers of Asteraceae.

limb: the upper, free, spreading portion of a corolla or perianth that is connate at the base.

linear: very narrow in relation to the length, and with the sides parallel. Fig. 23.

lithophyte: a plant that grows on the surface of unweathered rock.

loculicidal: *of the dehiscence of a fruit*, along lines coinciding with the centres of loculi. cf. **septicidal.**

loculus: an enclosed compartment within an organ e.g. an ovary, an anther. pl. **loculi.**

lodicule: one of a pair of tiny scales in a grass floret, between the lemma and the fertile parts of the flower, which may be reduced perianth segments.

lomentum: a legume having distinct constrictions or lines of abscission between the seeds and breaking into one-seeded segments when mature.

lyrate: deeply lobed, with a large terminal lobe and smaller lateral ones. Fig. 24.

macrospore: = **megaspore.**

mallee: a growth habit in which several woody stems arise separately from a lignotuber (usually applied to shrubby eucalypts); a plant having the above growth habit.

marginal: occurring at or very close to the margin.

megagametophyte: a plant body or cell lineage, formed by vegetative growth of the megaspore, that produces the female gametes of a heterosporous plant.

megasporangium: the larger of the two kinds of sporangia produced in the sexual life cycle of a heterosporous plant.

megaspore: the larger of the two kinds of spores produced in the sexual life cycle of a heterosporous plant, giving rise to the female gametophyte.

megasporophyll: a specialised leaf upon (or in the axil of) which one or more megasporangia are borne.

meiosis: the two-stage division of a diploid nucleus, occurring once in every sexual life cycle, in which gene recombination occurs and the number of chromosomes characteristic of the sporophyte plant is halved prior to the production of gametes.

mericarp: one segment of a fruit that breaks at maturity into units derived from the individual carpels. cf. **schizocarp.**

meristem: growing regions of a plant in which cells that have retained their embryonic characteristics, or reverted to them secondarily, divide to produce new cells.

mery: the number of parts per whorl that characterises a particular flower (generally constant for the perianth whorls and less often for the whorl(s) of stamens also). adj. **merous.**

mesocarp: the fleshy portion of the wall of a succulent fruit inside the skin and outside the stony layer, if any, surrounding the seed(s).

mesophyll: photosynthetic tissue of a green plant; *of vegetation*, characteristic of moist habitats and with soft, fairly large leaves predominating; a leaf whose area is within the approximate range 20–180 square cm.

microgametophyte: a plant body or cell lineage, formed by vegetative growth of the microspore, that produces the male gametes of a heterosporous plant.

micropyle: a small canal through the integument(s) of an ovule, persisting as a pore in the seed coat.

microsporangium: the smaller of the two kinds of sporangia produced in the sexual life cycle of a heterosporous plant.

microspore: the smaller of the two kinds of spores produced in the sexual life cycle of a heterosporous plant, giving rise to the male gametophyte.

microsporophyll: a specialised leaf upon (or in the axil of) which one or more microsporangia are borne.

midrib: the central, and usually the most prominent, vein of a leaf or leaf-like organ.

monadelphous: *of stamens*, united by their filaments into one bundle.

monocarpic: flowering and fruiting only once during its life span.

monochasium: a cymose inflorescence with the branches arising singly. cf. **dichasium.**

monochlamydeous: *of a flower*, having only one whorl of perianth parts.

monocotyledon: a flowering plant whose embryo has only one cotyledon (seed leaf). cf. **dicotyledon.**

monoecious: having the male and female reproductive structures in separate flowers but on the same plant. cf. **dioecious.**

monophyletic: derived from a single ancestral line. cf. **polyphyletic.**

monopodial: *of growth*, with a persistent terminal growing point producing many lateral organs successively; *of a stem*, growing in the above manner. cf. **sympodial.**

monotypic: containing only one taxon of the next lower rank (e.g. applied to a family containing only one genus). cf. **polytypic.**

morphology: the form and structure of an organism or part of an organism; the study of form and structure.

motile: actively moving; self-propelled.

mucilage: slimy material exuded by certain plants or plant organs. adj. **mucilaginous.**

mucro: a sharp, abrupt terminal point. adj. **mucronate**. Fig. 23.

muricate: rough on the surface due to minute, hard outgrowths of the epidermis.

mycorrhiza: a symbiotic union between a fungus and a plant root.

naked: *of sporangia*, not covered by an indusium; *of seeds*, exposed on the surface of a sporophyll (not enclosed within an ovary); *of flowers*, without perianth; *of protoplasts or gametes*, not bounded by a cell wall.

nectary: a gland that secretes nectar. adj. **nectariferous.**

neotype: a specimen selected to serve in place of a holotype where none of the material to which the name was originally applied is known to have been preserved.

nerve: a vein.

neuter: sterile (e.g. of flowers in which neither the androecium nor the gynoecium is functional in reproduction).

nocturnal: *of flowers*, opening only at night.

node: the level (transverse plane) of a stem at which one or more leaves arise.

nomen conservandum: a name of a family or genus (or taxon intermediate between these two) that has been formally accepted as the correct name contrary to the usual principles of botanical nomenclature.

nomen illegitimum: a name which, at the time of its publication, was superfluous (because the taxon to which it was applied had already been named) or had already been applied to another plant.

nomen nudum: a name published without a diagnosis or description of the entity to which it applies, and without reference to either.

nomen rejiciendum: a name rejected in favour of a 'nomen conservandum'.

nucellus: the central tissue of an ovule, within which the megaspore mother cell is formed.

nut: a hard, dry, indehiscent fruit formed from two or more carpels but containing only one seed.

obconical: cone-shaped but attached at the narrower end.

obcordate: *of a leaf blade*, broad and notched at the tip; heart-shaped but attached at the pointed end. Fig. 23.

oblanceolate: similar in shape to **lanceolate** but attached at the narrower end.

obligate: *of parasites*, unable to survive without the host. cf. **facultative.**

oblique: *of a leaf or leaflet*, larger on one side of the midrib than on the other, i.e. asymmetrical. Fig. 23.

obloid: (a three-dimensional shape) with short, parallel sides and rounded ends, as if composed of two hemispheres linked together by a very short cylinder.

oblong: having the length greater than the width but not many times greater, and the sides parallel. Fig. 23.

obovate: similar in shape to **ovate** but attached at the narrower end. Fig. 23.

obsolescent: non-functional but not reduced to a rudiment.

obsolete: reduced to a rudiment, or completely lacking.

obtuse: blunt or rounded at the apex, the converging edges separated by an angle greater than 90 degrees. Fig. 23.

ochrea: a sheath, formed from two stipules, encircling the node in Polygonaceae.

ontogeny: the development of a single organism, i.e. the sequence of stages through which it passes during its lifetime.

operculum: a lid or cover becoming detached at maturity by abscission; *in Eucalyptus (for example)*, a cap covering the bud and formed by fusion or cohesion of perianth parts.

opposite: *of leaves*, borne at the same level but on opposite sides of the stem; *of floral parts*, on the same radius (as). cf. **alternate.**

orbicular: circular or nearly so. Fig.23.

order: a taxonomic grouping of families believed to be closely related (sometimes a single family with no apparent close relatives).

orthotropous: *of an ovule*, erect so that the micropyle points away from the placenta. Fig. 25.

ovary: the basal portion of a carpel or group of fused carpels, enclosing the ovule(s).

ovate: shaped like a section through the long axis of an egg, and attached by the wider end. Fig. 23.

ovoid: egg-shaped (in three dimensions). cf. **ovate.**

ovulate: with ovules.

ovule: a structure in a seed plant within which one or more megaspores are formed and which develops into a seed after fertilisation.

ovuliferous: bearing ovules (e.g. applied to scales in a megasporangiate cone in gymnosperms).

palea: *in a grass floret*, the upper one of the two bracts enclosing a flower.

palmate: *of a leaf*, divided into several leaflets which arise at the same point. Fig. 24.

palmatifid: *of a leaf*, deeply divided into several lobes which arise (almost) at the same level. Fig. 24.

palmatisect: a condition intermediate between **palmate** and **palmatifid**, with the green tissue of the lamina completely divided into several segments, but the segments not fully separated at the base. Fig. 24.

palynology: the scientific study of pollen.

panicle: a compound raceme; an indeterminate inflorescence in which the flowers are borne on branches of the main axis or on further branches of these.

paniculate: indeterminate and much branched.

papilla: a small, elongated protuberance on the surface of an organ, usually an extension of one epidermal cell. adj. **papillose.**

pappus: a tuft (or ring) of hairs or scales borne above the ovary and outside the corolla in Asteraceae and possibly representing the calyx; a tuft of hairs on a fruit.

parasite: an organism living on or in a different organism and deriving nourishment from it. cf. **saprophyte, epiphyte.**

paratype: a specimen, other than the holotype, that was cited with the original publication of a name.

parenchyma: plant tissue consisting of mature, living cells that are relatively unspecialised in function.

parietal: attached to the margins of a structure; *of placentation*, having the ovules attached to placentas on the wall of the ovary. Fig. 25.

paripinnate: having an even number of pinnae by virtue of having a pair in the terminal position. cf. **imparipinnate**. Fig. 24.

-partite: divided, almost to the base, into segments (commonly applied to a style).

pedicel: the stalk of a flower. adj. **pedicellate.**

peduncle: the stalk of an inflorescence; *in ferns*, the stalk of a sporocarp. adj. **pedunculate.**

pellucid: transparent.

peltate: *of a leaf*, having the stalk attached to the lower surface of the blade, not to the margin (also applied, in the same sense, to other stalked structures). Fig. 23.

pendulous: drooping; *of ovules*, attached at the top of the ovary and hanging downwards from an apical placenta.

penicillate: pencil-shaped; tufted like an artist's brush.

penniveined: with conspicuous lateral veins diverging from the midrib and lying approximately parallel to each other.

pentamerous: *of a flower*, having five parts in each floral whorl (not necessarily including the gynoecium).

perennate: maintain a dormant, vegetative state throughout non-growing seasons.

perennial: a plant whose life span extends over more than two growing seasons.

perfoliate: *of a sessile leaf or bract*, having its base completely wrapped around the stem.

perianth: the calyx and corolla of a flower, especially where the two are similar.

pericarp: the wall of a fruit, developed from the ovary wall.

perigynous: *of perianth segments and stamens*, arising from a cup or tube (hypanthium) that is free from the ovary but extending above its base. cf. **hypogynous, epigynous**. Fig. 26.

perisperm: nutritive tissue in an angiospermous seed, formed from the nucellus. cf. **endosperm.**

persistent: remaining attached to the plant beyond the expected time of falling (e.g. of sepals not falling after flowering).

petal: a member of the inner whorl of non-fertile parts surrounding the fertile organs of a flower, usually soft and coloured conspicuously.

petaloid: like a petal; soft in texture and coloured conspicuously.

petiole: the stalk portion of a leaf.

petiolule: the stalk portion of a leaflet.

phanerogam: (literally) a plant with conspicuous reproductive parts; a plant reproducing by seeds. cf. **cryptogam.**

phenotype: the physical characteristics of an organism; the outward expression of characteristics conferred on an organism by its genotype.

phloem: the tissue in the conducting system of a plant through which metabolites (products of chemical reactions in the plant) are transported.

phylloclade: a very leaf-like, photosynthetic stem of a plant whose true leaves are much reduced. cf. **cladophyll.**

phyllode: a leaf whose blade is much reduced or absent, and whose petiole and rachis have assumed the functions of the whole leaf. cf. **cladode.**

phyllotaxy: the arrangement of leaves on a stem (when spiral, often expressed quantitatively as the fraction of the circumference of the stem that separates two successive leaves).

phylogeny: the evolutionary development of a plant group, i.e. its derivation from its ancestors and the relationship among its members. adj. **phylogenetic.**

phylum: a taxon of high rank, the major unit of classification. cf. **division.**

pilose: hairy, the hairs soft and clearly separated but not sparse.

pinna: a primary segment of the blade of a compound leaf.

pinnate: divided into pinnae; once-compound. cf. **bipinnate**. Fig. 24.

pinnatifid: cut deeply into lobes that are spaced out along the axis (of the leaf). cf. **palmatifid**. Fig. 24.

pinnatisect: dissected down to the midrib but having the segments confluent with it. Fig. 24.

pinnule: a leaflet of a bipinnate leaf.

pistil: a free carpel or a group of fused carpels.

pistillode: a sterile pistil, often rudimentary.

pith: the central region of a stem, inside the vascular cylinder.

placenta: a region, within an ovary, to which ovules are attached.

placentation: the arrangement of placentas, and hence of ovules, within an ovary. Fig. 25.

plicate: folded back and forth longitudinally like a fan.

plumose: like a feather; with fine hairs branching from a central axis.

plumule: the portion of an embryo that gives rise to the shoot system (as distinct from the root system) of a plant. cf. **radicle.**

pod: a leguminous fruit.

pollen: the microspores of seed plants; the powdery mass of microspores shed from anthers.

pollen-sac: see **sac.**

pollination: the transfer of pollen from the male organ, where it is formed, to the receptive region of a female organ, e.g. from anther to stigma.

pollinium: a cohering mass of pollen grains, transferred as a unit in pollination. pl. **pollinia.**

polygamodioecious: having bisexual and male flowers on some plants, and bisexual and female flowers on others.

polygamous: having bisexual and unisexual flowers on the same plant.

polymorphic: having more than two distinct morphological variants.

polypetalous: with free petals. cf. **gamopetalous.**

polyphyletic: composed of members that originated, independently, from more than one evolutionary line. cf. **monophyletic.**

polyploid: having more than two of the basic sets of chromosomes in the nucleus.

polytypic: containing more than one taxon of the next lower rank. cf. **monotypic.**

pome: a fleshy (false) fruit, formed from an inferior ovary, in which the receptacle or hypanthium has enlarged to enclose the true fruit.

posterior: *of floral parts*, on the side of the flower nearest to the axis. cf. **anterior.**

prickle: a hard, pointed outgrowth from the surface of a plant, involving several layers of cells but not containing a vein.

procumbent: trailing or spreading along the ground but not rooting at the nodes.

propagule: a structure with the capacity to give rise to a new plant, e.g. a seed, a spore, part of the vegetative body capable of independent growth if detached from the parent.

prophyll: a leaf formed at the base of a shoot, usually smaller than those formed subsequently.

prostrate: lying flat on the ground.

protandrous: having the male sex organs maturing before the female; *of a flower*, shedding the pollen before the stigma is receptive. cf. **protogynous.**

prothallus: a gametophyte body, especially in ferns and related plants.

protogynous: having the female sex organs maturing before the male; *of a flower*, shedding the pollen after the stigma has ceased to be receptive. cf. **protandrous.**

proximal: near to the point of origin or attachment. cf. **distal.**

pseudo-: false; apparent but not genuine.

puberulous: covered with minute, soft, erect hairs.

pubescent: covered with short, soft, erect hairs.

pulvinus: a swelling at the base of the stalk of a leaf or leaflet, often glandular or responsive to touch.

punctate: marked with dots.

pungent: ending in a stiff, sharp point; having an acrid taste or smell.

pyrene: the 'stone' (endocarp plus seed) of a succulent fruit. cf. **drupe.**

quincuncial: *of the arrangement of corolla lobes in a bud,* a variant of imbricate aestivation. Fig. 25.

raceme: an indeterminate inflorescence in which a main axis produces a series of flowers on lateral stalks, the oldest at the base and the youngest at the top. adj. **racemose.**

rachilla: the axis of a grass spikelet, above the glumes.

rachis: the axis of an inflorescence or a pinnate leaf; pl. **rachises. secondary rachis:** the axis of a pinna in a bipinnate leaf.

radical: *of leaves*, clustered at the base of the stem.

radicle: the portion of an embryo that gives rise to the root system of a plant. cf. **plumule.**

raphe: the part of the stalk of an anatropous ovule that is fused along the side of the ovule.

raphides: needle-like crystals that occur in bundles in the vacuoles of some plant cells.

ray: a zygomorphic flower in Asteraceae; a radial band of cells traversing the conducting elements in woody stems.

receptacle: the axis of a flower (= **torus**); *in ferns*, an axis on which sporangia arise.

recurved: curved or curled downwards or backwards.

reflexed: bent sharply downwards or backwards.

regular: see **actinomorphic.**

reniform: kidney-shaped. Fig. 23.

replum: a longitudinal partition in an ovary, formed between parietal placentas.

resupinate: twisted through 180 degrees, e.g. as with the ovary of most Orchidaceae.

reticulate: forming a network.

retinaculum: a hook-like structure to which another structure is tethered; *in Orchidaceae and Asclepiadaceae*, the structure to which pollen masses are attached; *in Acanthaceae*, the persistent stalk of an ovule.

retrorse: directed backwards or downwards. cf. **antrorse.**

retuse: with a very blunt and slightly notched apex. Fig. 23.

revolute: rolled downwards or backwards.

rhachilla: = rachilla.

rhachis: = rachis.

rhizoid: a thread-like, unicellular absorbing structure, occurring in fern gametophytes and in some non-vascular plants.

rhizome: an underground stem, usually growing horizontally.

rhizophore: *in Selaginella*, a leafless stem that produces roots.

rhomboid: quadangular, with the lateral angles obtuse. Fig. 23.

root: a unit of the axial system of a plant which is usually underground, does not bear leaves, tends to grow downwards and is typically derived from the radicle of the embryo. See **adventitious.**

rootstock: a short, erect, swollen structure at the junction of the root and shoot systems of a plant.

rostellum: a beak-like upward extension of the stigma in Orchidaceae.

rotate: circular and flattened, e.g. of a corolla with a very short tube and spreading lobes.

rudimentary: poorly developed and not functional. cf. **vestigial, obsolete.**

rugose: deeply wrinkled.

ruminate: mottled in appearance, e.g. of bark, or of the food reserves in a seed.

runcinate: deeply lobed and with the lobes slanted away from the apex. Fig. 24.

runner: a slender, prostrate or trailing stem which produces roots and sometimes erect shoots at its nodes.

sac: a pouch or cavity; **pollen-sac:** a cavity, in an anther, in which pollen is formed; **embryo-sac:** a large, multi-nucleate cell in which an egg nucleus is formed and fertilised, and in which an embryo begins to develop.

saccate: pouched.

sagittate: shaped like an arrow-head. Fig. 23.

samara: a dry, indehiscent fruit with its wall expanded into a wing.

saprophyte: an organism deriving its nourishment from dead organic matter and usually lacking chlorophyll. cf. **parasite.**

scabrid (= scabrous): rough to the touch.

scale: a reduced or rudimentary leaf, e.g. surrounding a dormant bud; a thin flap of tissue, e.g. on the ventral surface of a liverwort thallus and at the base of a stamen in Simaroubaceae.

scandent: climbing.

scape: the stem-like, flowering stalk of a plant with radical leaves.

scarious: dry and membranous.

schizocarp: a dry fruit formed from more than one carpel but breaking apart into 1-carpel units when ripe.

sclerenchyma: mechanical tissue with heavily thickened cell walls.

scleromorph: a plant whose leaves (or stems, if leafless) are hard in texture, usually having thick cuticle and containing many fibres. cf. **xeromorph.**

sclerophyllous: with leaves stiffened by sclerenchyma.

scorpioid: *of a cymose inflorescence*, branching alternately on one side and then the other. cf. **helicoid.**

secund: with all the parts grouped on one side or turned to one side (applied especially to inflorescences).

seed: a propagating organ formed in the sexual reproductive cycle of gymnosperms and angiosperms, consisting of a protective coat enclosing an embryo and food reserves.

segment: a part or sub-division of a divided organ; one of a group of similar organs named collectively, e.g. one petal = a segment of a corolla.

sepal: a member of the (usually green) outer whorl of non-fertile parts surrounding the fertile organs of a flower.

sepaloid: looking like sepals, e.g. *of bracts*, usually green and arranged in a ring beneath a flower.

septate: divided internally by partitions.

septicidal: *of the dehiscence of a fruit*, along lines coinciding with the partitions between loculi. cf. **loculicidal.**

septum: a partition. pl. **septa.**

seriate: in rows or whorls.

sericeous: silky; covered with silky hairs.

serrate: toothed, with asymmetrical teeth pointing forward. Fig. 24.

serrulate: finely serrate. Fig. 24.

sessile: without a stalk (when applied to a stigma, indicates that the style is absent, the stigma being 'sessile' on the ovary).

seta: a bristle or stiff hair; *in Bryophyta*, the stalk portion of a sporophyte plant body. **terminal seta:** an appendage to the tip of an organ, e.g. the primary rachis of a bipinnate leaf in *Acacia*.

setose: bristly.

shrub: a woody plant less than 5 metres high, either without a distinct main axis, or with branches persisting on the main axis almost to its base.

siliceous: containing silica.

silicula: a short siliqua, not more than twice as long as its width.

siliqua: a dry, dehiscent fruit formed from a superior ovary of two carpels, with two parietal placentas and divided into two loculi by a false septum between the placentas.

simple: undivided; *of a leaf*, not divided into leaflets; *of a hair or an inflorescence*, not branched.

sinuate: with deep, wave-like depressions along the margin. cf. **undulate**. Fig. 24.

sinus: a notch or depression in the margin of an organ.

solitary: *of flowers*, borne singly, not grouped in an inflorescence.

sorus: *in ferns*, a discrete group of sporangia. pl. **sori.**

spadix: a spicate inflorescence with a stout, often succulent axis.

spathaceous: like a spathe; with a spathe.

spathe: a large bract ensheathing an inflorescence.

spathulate (= spatulate): spoon-shaped; broad at the tip and narrowed towards the base. Fig. 23.

species: a taxon comprising individuals, or populations of individuals, capable of interbreeding to produce fertile offspring; the largest group of individuals between which there are no distinguishable, consistent differences in form or reproductive mechanisms.

spike: an unbranched, indeterminate inflorescence in which the flowers are without stalks. adj. **spicate.**

spikelet: a unit of the inflorescence in grasses, sedges and some other monocotyledons, consisting of one to many flowers and associated glumes.

spine: a stiff, sharp-pointed structure, formed by modification of a plant organ, e.g. a lateral branch or a stipule.

spinescent: ending in a spine; modified to form a spine.

spinose: bearing spines.

spiral: *of leaves or floral organs*, borne at different levels on the axis, in an ascending spiral. cf. **cyclic.**

sporangiophore: the stalk of a sporangium.

sporangium: a structure within which spores are formed. pl. **sporangia.**

spore: a simple propagule, produced either sexually or asexually, and consisting of one or a few cells.

sporocarp: a fruiting body containing sporangia.

sporogenous: *of cells or tissues*, in which spores are formed.

sporophyll: a specialised leaf-like organ on which one or more sporangia are borne.

sporophyte: a plant, or phase of a life cycle, that bears the spores formed during the sexual reproductive cycle.

spur: a tubular pouch at the base of a perianth part, often containing nectar.

stamen: one of the male organs of a flower, consisting typically of a stalk (filament) and a pollen-bearing portion (anther). adj. **staminate.**

staminode: a sterile stamen, often rudimentary.

standard: the posterior petal in the flower in Fabaceae.

stellate: star-shaped; consisting of star-shaped cells.

stem: the main axis or a branch of the main axial system of a plant, developed from the plumule of the embryo and typically bearing leaves.

stigma: the pollen-receptive surface of a carpel or group of fused carpels, usually sticky.

stipe: a small stalk; *in ferns*, the petiole of a frond; *in algae*, the cylindrical basal portion of a thallus.

stipitate: stalked; borne on a stipe; *of an ovary*, borne on a gynophore.

stipule: one of a pair of appendages at the bases of leaves in many dicotyledons.

stolon: a prostrate or trailing stem that produces roots at the nodes.

stoloniferous: having stolons; trailing over the soil surface and rooting at the nodes.

stoma: a pore; a pore in the epidermis of a leaf or other aerial organ, providing access for gaseous exchange between the tissues and the atmosphere. pl. **stomata.**

stomium: a region of dehiscence, e.g. of an anther in flowering plants or of a capsule in mosses. pl. **stomia.**

striate: striped with parallel longitudinal lines or ridges.

strigose: with sharp, stiff hairs which are slanting rather than erect.

strobilus: a 'cone' consisting of sporophylls borne close together on an axis.

strophiole: = **caruncle.**

style: an elongated part of a carpel, or group of fused carpels, between the ovary and the stigma.

subulate: narrow and tapering gradually to a fine point. Fig. 23.

sulcate: grooved; furrowed.

superior: *of an ovary*, borne above the level of attachment of the other floral parts, or above the base of a cup (hypanthium) that is free from the ovary and bears the perianth segments and stamens. cf. **inferior**. Fig. 26.

suture: a line of junction between two fused organs; a line of dehiscence.

syconium: a multiple fruit with a hollow centre, e.g. in *Ficus* (fig).

sympatric: *of two or more species*, having coincident or ovarlapping ranges of distribution. cf. **allopatric.**

sympetalous: = **gamopetalous.**

sympodial: *of growth*, without a single, persistent growing point; changing direction by frequent replacement of the growing apex by a lateral growing point below it; *of a stem*, growing in the above manner. cf. **monopodial.**

synandrium: an androecium with the anthers of the stamens cohering. cf. **syngenesious.**

syncarpous: *of a flower*, having two or more carpels, all fused together.

syngenesious: *of the stamens of one flower*, fused together by the anthers e.g. in Asteraceae.

syntype: one of two or more specimens cited by the author at the time of publication of a name for which no holotype was designated.

taproot: the main, descending root of a plant that has a single, dominant root axis.

taxon: a group or category, at any level, in a system for classifying plants or animals.

tendril: a slender climbing organ formed by modification of a part of a plant, e.g. a stem, a leaf or leaflet, a stipule.

tepal: a perianth segment in a flower in which all the perianth segments are similar in appearance.

terete: cylindrical or nearly so; circular in cross-section.

terminal: at the apex or distal end.

ternate: in groups of three; *of leaves*, arranged in whorls of three; *of a single leaf*, having the leaflets arranged in groups of three. Fig. 24.

terrestrial: of or on the ground; *of the habitat of a plant*, on land as opposed to in water, or on the ground as opposed to on another plant.

testa: a seed coat.

tetrad: a group of four; four pollen grains remaining fused together at maturity, e.g. in Ericaceae, Epacridaceae.

tetradynamous: *of an androecium*, consisting of four stamens of the same length and two of a different length.

tetramerous: *of a flower*, having four segments in each perianth whorl, and usually in each whorl of stamens also.

thallus: the vegetative body of a plant that is not differentiated into organs such as stems and leaves, e.g. algae, the gametophytes of many liverworts, and Lemnaceae.

thorn: a modified plant organ, especially a stem, that is stiffened and terminates in a pungent point.

throat: *of a corolla tube*, the top, where the tube joins the lobes.

thyrse: a branched inflorescence in which the main axis is indeterminate and the lateral branches determinate in their growth.

tomentum: a covering of dense, matted, woolly hairs. adj. **tomentose.**

torus: see **receptacle.**

trabecula: a transverse partition dividing or partly dividing a cavity.

tree: a woody plant at least 5 metres high, with a main axis the lower part of which is usually unbranched.

trichome: an unbranched epidermal outgrowth, e.g. a hair, a papilla; *in blue-green algae*, a single row of cells in a filamentous colony.

trichotomous: branching almost equally into three parts.

trifid: deeply divided into three parts.

trifoliate: having three leaves.

trifoliolate: *of a leaf*, having three leaflets.

trigonous: triangular in cross-section and obtusely-angled. cf. **triquetrous.**

trimerous: *of a flower*, having three segments in each perianth whorl and usually in each whorl of stamens also.

tripinnate: *of leaves*, thrice pinnately divided.

triquetrous: triangular in cross-section and acutely-angled; with three distinct longitudinal ridges. cf. **trigonous.**

truncate: with an abruptly transverse end, as if cut off. Fig. 23.

tuber: a storage organ formed by swelling of an underground stem or the distal end of a root.

tubercle: a small wart-like outgrowth.

tuberculate: covered with tubercles.

tuberous: swollen; *of roots*, tuber-like.

turgid: swollen due to high water content. cf. **flaccid.**

type: a designated representative of a plant name.

umbel: a racemose inflorescence in which all the individual flower stalks arise in a cluster at the top of the peduncle and are of about equal length.

undulate: wavy, i.e. not flat. cf. **sinuate**. Fig. 24.

unifoliate: having one leaf.

unifoliolate: *of a leaf*, basically compound, but reduced to only one leaflet.

unilocular: *of an ovary, anther or fruit*, having only one internal cavity.

unisexual: bearing only male or only female reproductive organs.

united: fused together.

urceolate: urn-shaped.

utricle: a small bladder; a membranous bladder-like sac enclosing an ovary or fruit.

valvate: *of sepals or petals in a bud*, meeting edge to edge, not overlapping. cf. **imbricate**. Fig. 25.

valve: a portion of an organ that has fragmented; *of a capsule*, the teeth-like portions into which the dehiscing part of the pericarp splits at maturity.

vascular: specialised for conduction of fluids; **vascular plants:** plants containing specialised conducting tissues.

vein: a strand of vascular tissue.

velamen: a water-retaining outer layer of the aerial roots of some epiphytes, especially orchids.

velum: a membranous covering; a veil.

venation: the arrangement of veins in a leaf.

ventral: *of a lateral organ*, facing towards the subtending axis; *of a thallus*, facing towards the substratum. cf. **dorsal.**

vernation: the arrangement of unexpanded leaves in a bud. cf. **aestivation.**

versatile: *of anthers*, swinging freely about the point of attachment to the filament, which is approximately central.

verticillate: arranged in one or more whorls.

vesicle: a bladder-like sac or cavity filled with gas or liquid.

vessel: a capillary tube formed from a series of open-ended cells in the water-conducting tissue of a plant.

vestigial: reduced from the ancestral condition and no longer functional. cf. **rudimentary.**

villous: shaggy with long, weak hairs.

viscid: *of a surface*, sticky; coated with a thick, syrupy secretion.

viscous: *of a liquid*, not pouring freely; having the consistency of syrup or honey.

viviparous: *of seeds or fruits*, germinating before being shed from the parent plant.

whorl: a ring of leaves, bracts or floral parts borne at the same level on an axis.

wing: a membranous expansion of a fruit or seed, which aids dispersal; a thin flange of tissue extended beyond the normal outline of a stem or petiole; a lateral petal of a flower in Fabaceae.

xeromorph: a plant having structural features usually associated with plants of arid habitats (such as hard or succulent leaves) but not necessarily drought-tolerant. cf. **xerophyte.**

xerophyte: a drought-tolerant plant.

xylem: the tissue, in a vascular plant, that conducts water and mineral salts from the roots to the leaves.

zygomorphic: *of a flower or calyx or corolla*, symmetrical about one plane only, usually the plane that bisects the flower vertically. cf. **actinomorphic.**

Figures 23. A–P–Leaf shapes: A–subulate; B–acicular; C–filiform; D–linear; E–oblong; F–falcate; G–lanceolate; H–elliptic; I–ovate; J–obovate; K–orbicular and peltate; L–deltoid; M–rhomboid; N–cuneate; O–reniform; P–spathulate. Q–V–Leaf bases: Q–cordate; R–hastate; S–sagittate; T–auriculate; U–oblique; V–truncate. W–GG–Leaf tips: W–aristate; X–caudate; Y–acuminate; Z–acute; AA–cuspidate; BB–mucronate; CC–apiculate; DD–obtuse; EE–retuse; FF–emarginate; GG–obcordate.

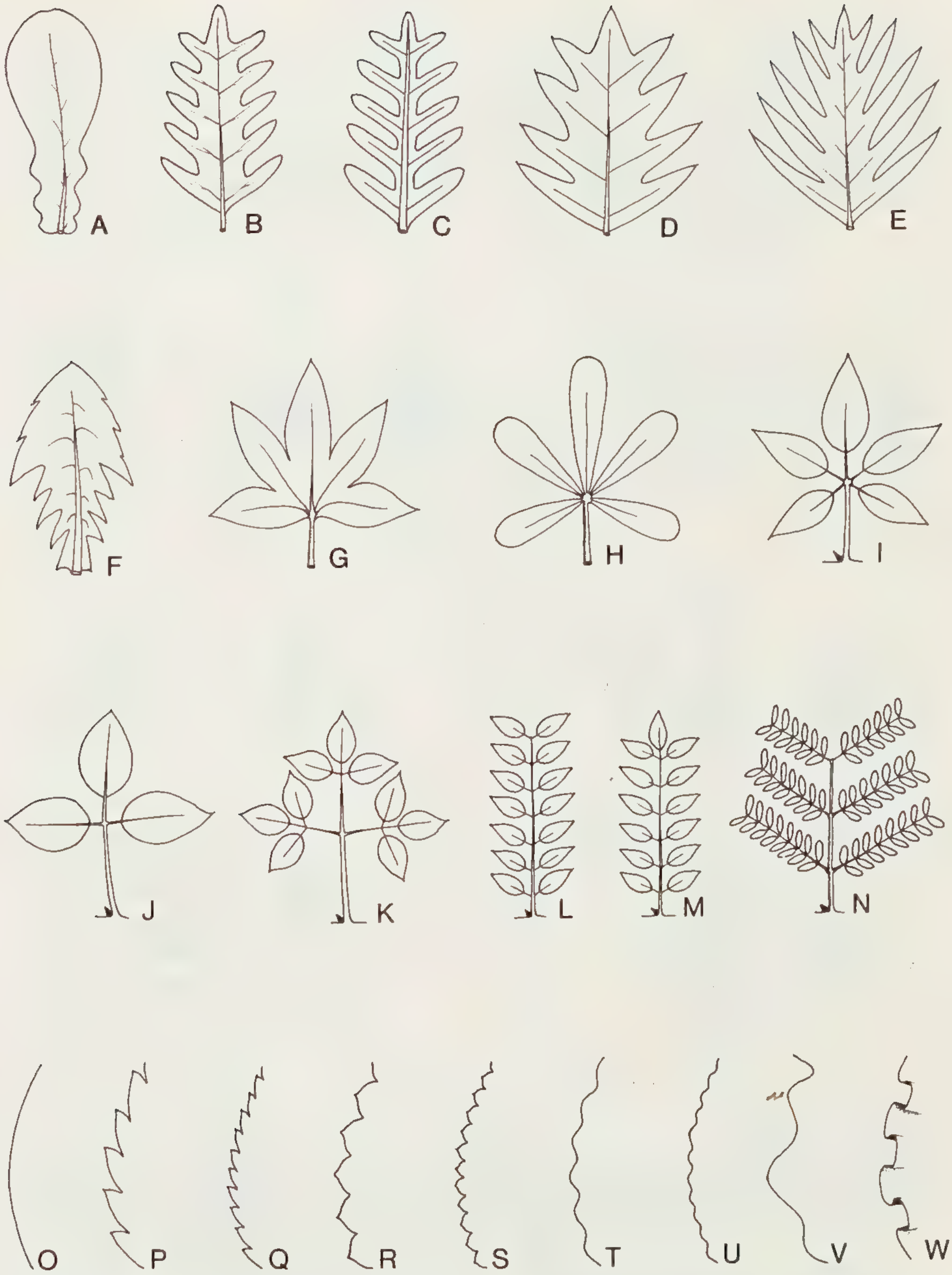

Figure 24. Division of leaves: A–lyrate; B–pinnatifid; C–pinnatisect; D–incised; E–laciniate; F–runcinate; G–palmatifid; H–palmatisect (= digitate); I–palmate; J–trifoliolate; K–ternate (strictly, biternate); L–M–pinnate (L–paripinnate, M–imparipinnate); N–bipinnate; O–entire; P–serrate; Q–serrulate; R–dentate; S–denticulate; T–crenate; U–crenulate; V–sinuate; W–undulate.

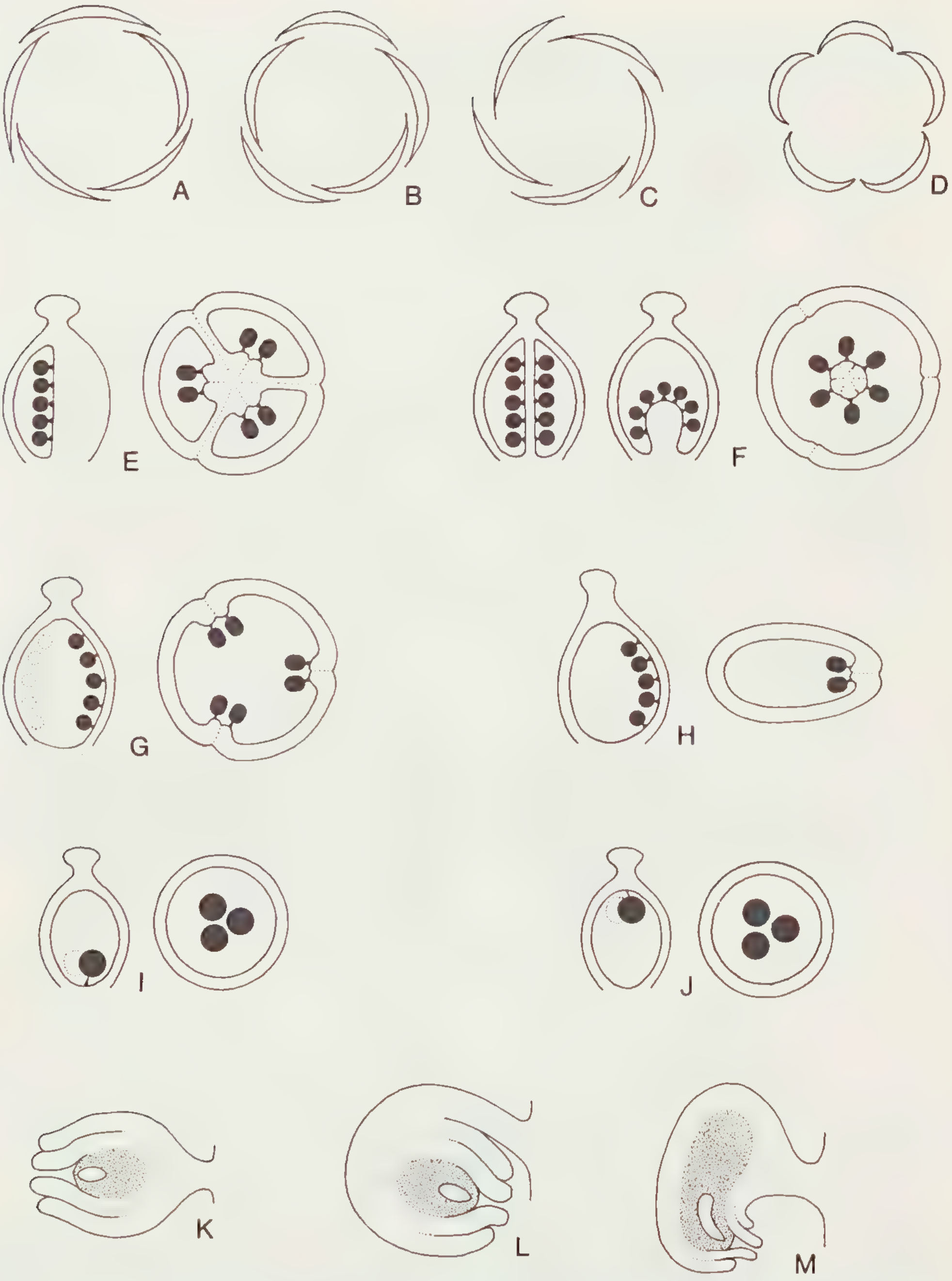

Figure 25. A–D–Aestivation: A–C–imbricate (A–cochlear, B–quincuncial, C–convolute); D–valvate. E–J–placentation: E–axile; F–free-central; G–parietal; H–marginal; I–basal; J–apical. K–M–Orientation of ovules: K–orthotropous; L–anatropous; M–campylotropous.

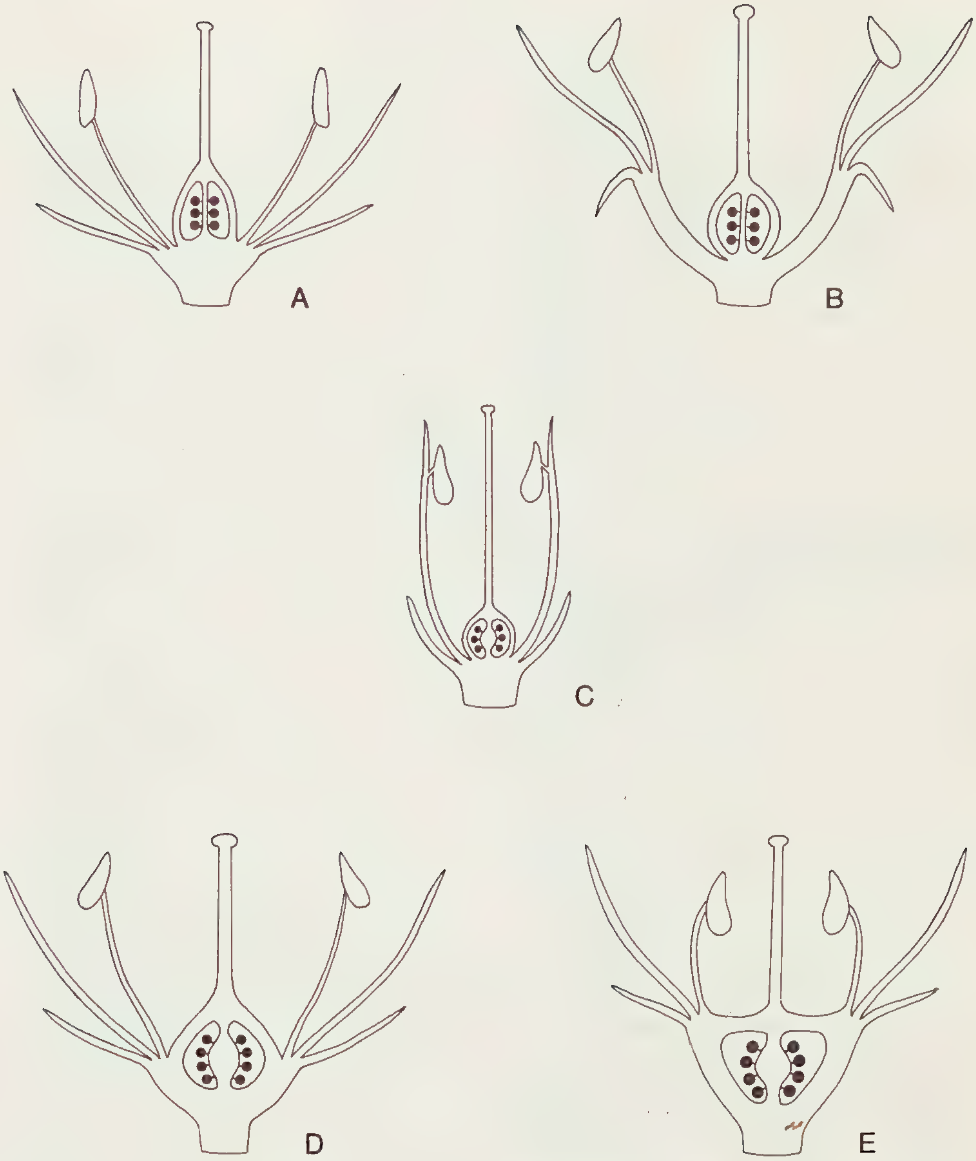

Figure 26. Positions of floral organs: A–perianth and stamens hypogynous, ovary superior; B–perianth and stamens perigynous, ovary superior; C–perianth and stamens hypogynous, stamens epipetalous, ovary superior; D–perianth and stamens epigynous, ovary half-inferior; E–perianth and stamens epigynous, ovary inferior.

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Lythraceae	18	Plumbaginaceae	5	Tamaricaceae	8
Magnoliaceae	2	Poaceae	43,44	Theaceae	6
Malpighiaceae	24	Podostemaceae	18	Thymelaeaceae	18
Malvaceae	7	Polemoniaceae	30	Tiliaceae	7
Marantaceae	45	Polygalaceae	24	Trapaceae	18
Melastomataceae	18	Polygonaceae	5	Tremandraceae	24
Meliaceae	26	Pontederiaceae	45	Triuridaceae	39
Melianthaceae	25	Portulacaceae	5	Tropaeolaceae	27
Menispermaceae	2	Posidoniaceae	39	Typhaceae	45
Menyanthaceae	30	Potamogetonaceae	39	Ulmaceae	3
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Moringaceae	8	Ranunculaceae	2	Viscaceae	22
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Myoporaceae	33	Restionaceae	40	Winteraceae	2
Myristicaceae	2	Rhamnaceae	24	Xanthophyllaceae	24
Myrsinaceae	10	Rhizophoraceae	22	Xanthorrhoeaceae	46
Myrtaceae	19,20,21	Rosaceae	10	Xyridaceae	40
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Nepenthaceae	8	Rutaceae	26	Zosteraceae	39
Nyctaginaceae	4	Salicaceae	8	Zygophyllaceae	26
Nymphaeaceae	2	Santalaceae	22		
Ochnaceae	6	Sapindaceae	25		
Olacaceae	22	Sapotaceae	10		
Oleaceae	32	Saxifragaceae	10		
Onagraceae	18	Scrophulariaceae	32		
Opiliaceae	22	Simaroubaceae	25		
Orchidaceae	47	Smilacaceae	46		
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Papaveraceae	2	Sphenocleaceae	34		
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Pedaliaceae	33	Stemonaceae	46		
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FLORA OF AUSTRALIA

The series *Flora of Australia,* planned to comprise approximately 50 volumes to be published over a 20-year period, is designed for use by persons with some botanical knowledge who require information on the names, characteristics, distribution and habitat of Australian plants.

George Bentham's *Flora Australiensis,* the only previous Australia-wide Flora, was written in England and published between 1863 and 1878. It contained 8125 species. The new *Flora,* written by many botanists, will describe all the native and naturalised plants of Australia, currently estimated to be over 20 000 species. Co-ordinated and edited by the Bureau of Flora and Fauna, Department of Home Affairs and Environment, it will contain keys for identification, colour and black and white illustrations and distribution maps.

This introductory volume contains chapters on the history and purpose of the *Flora of Australia* project, the origin and evolution of the Australian flora, and the systematic arrangement of plant families. It includes a key for the identification of families of flowering plants and a glossary of botanical terms.

Cover: *Helichrysum ayersii* F. Muell. and *Ptilotus obovatus* (Gaudich.) F. Muell., near the Cavenagh Range, central Western Australia (Photograph A. S. George).

R80/770(1) Cat. No. 810957 2